DISTRIBUTION, ABUNDANCE, AND GROWTH OF LARVAL WALLEYE POLLOCK (*THERAGRA CHALCOGRAMMA*) IN A GLACIATED FJORD

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Franz-Josef Müter

Fairbanks, Alaska

December 1992

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ABSTRACT

This is the first study to examine the early life history of walleye pollock (*Theragra chalcogramma*) in a glaciated fjord system. Ichthyoplankton samples were taken at 6 stations in Resurrection Bay during early May and early June 1989. Standard length of all walleye pollock were measured and subsamples from two stations were aged for growth rate and hatch date analysis.

Abundances ranged from 60 to 575 larvae m^{-2} in May and from 0 to 10 larvae m^{-2} in June with densities up to 12 larvae m^{-3} in May. The estimated growth rate was 0.18 mm/day. Hatching took place from early April until early May with a median hatch date on April 25.

The observed abundances and growth rate indicate that the deep fjord is a good nursery ground for larval walleye pollock. Hydrographic data and larval size distribution suggest that advection plays a major role in determining the distribution of larvae in the region.

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INTRODUCTION

Background

Fjords have long been recognized as nursery grounds for many commercially important fish species. There is ample evidence that fjords are generally utilized by a variety of fish populations and by all life stages (De Silva 1973, Lie 1978, Carmo Lopes 1979, Strickland 1983). Matthews and Heimdal (1980) in their review of food chains point out that many fjords along Scandinavian, Scottish and North American coasts are highly productive areas. Their productivity is often enhanced by hydrographic boundary conditions or fresh water runoff, which can increase nutrient levels. Estimates of secondary and tertiary production are scarce, but the few quantitative measurements show high ecological efficiencies can be achieved, particularly in outer areas of a fjord, where advection can increase prey densities (Matthews and Heimdal 1980). Production may be further enhanced by upwelling conditions which are common in many coastal areas at a fjords mouth. This is especially true for the southern coast of Alaska, where the relaxation of easterly winds promotes coastal divergence and upwelling in the summer months (Royer 1982). The hydrographic and meteorological conditions thus can make fjords areas of abundant food supply.

Many fish species exploit fjords during various stages of their life cycle. Rogers et al. (1986) in their review describe the nearshore zone of the Gulf of Alaska as an important spawning area and/or rearing area for several commercially important fish species, including *Clupea harengus pallasi, Theragra chalcogramma* and assorted Pleuronectidae. They conclude that "research on nearshore fish is needed in other areas of the Gulf . . . to accurately evaluate

environmental or fishery impacts". Ichthyoplankton surveys between 1976 and 1982 on the shelf off Kodiak island and several inshore bays identified 153 species from 33 families. The inshore bays of Kodiak island were used by larval and juvenile fishes of many species (Rogers et al. 1986). This clearly indicates that the inshore bays play an important role in the life cycle of these populations. In this study I showed that Resurrection Bay, and thus probably many other inlets along the northern boundary of the Alaskan gyre, are of similar importance to the larvae of *Theragra chalcogramma*.

Physical and biological processes within fjords are not separated from processes on the shelf and in other embayments. Advective exchanges with coastal waters influence the community structure within a fjord. Large variations in zooplankton abundances can result from estuarine circulation, density-driven flows and tidal exchanges (Stone 1980, Lewis and Thomas 1986, Lindahl and Hernroth 1988). The importance of advection in the recruitment to and/or retention within a fjord has not yet been demonstrated for fish larvae. However, since physical processes within fjords are linked to larger scale processes on the shelf (Klinck et al. 1982), the dynamics of a larval fish population within a fjord should be related to environmental conditions over the adjacent shelf.

The target species

I chose walleye pollock as target species in this study for several reasons:

1. The abundance of walleye pollock larvae in Resurrection Bay during the spring 1989 collections was higher than that of any other species.
2. The development and early life history of walleye pollock in other areas of the Gulf is well known (Kendall et al. 1987,

Dunn and Matarese 1987, Kim 1989)

3. Walleye pollock is a commercially important species with annual landings off Alaska exceeding one million metric tons (Lloyd and Davis 1989).

4. Walleye pollock populations show high fluctuations in year-class strength (Megrey 1991) which creates a strong incentive to determine possible causes.

Research on walleye pollock in the northern Gulf of Alaska has thus far concentrated on the Shelikof Strait region, while other areas along the Gulf, except for Auke Bay in southeastern Alaska (Haldorson et al. 1989a, b), have received little attention. Although the Shelikof Strait spawning area is believed to be the most important in the Gulf of Alaska (Hinckley et al. 1991) it is not clear whether extensive pollock spawning occurs in other areas of the Gulf or its embayments. Smith et al. (1991) observed high densities of larval walleye pollock in Resurrection Bay in 1988. Norcross (unpubl. data) found concentrations of them in adjacent Prince William Sound that approach those reported from Shelikof Strait. There is also evidence of a large spawning area to the northeast of Kodiak island from data presented by Rugen (1990). His figures show that larval densities upstream of Shelikof Strait were of the same order of magnitude as those inside the Strait for the second half of May, averaged over several years. These high concentrations must originate on the shelf upstream from Kodiak Island.

Kim and Gunderson (1988) in their synopsis of the biology of walleye pollock state that the distribution of spawning pollock in the Gulf shows the highest abundance in areas where the coastline is indented, providing sheltered areas. This makes the bays and fjords along the coast, both upstream and downstream from Shelikof Strait,

potentially important nursery areas for walleye pollock larvae and/or juveniles.

The early life history of walleye pollock in the western Gulf of Alaska has been studied extensively (Kendall et al. 1987, Kim and Gunderson 1988, Kim 1989). Peak spawning in the Shelikof Strait region occurs from the end of March to early April and incidental spawning persists into late May. The spawning time shows little variation between years. The pelagic eggs are spawned at depth (>200 m) and have about a two week incubation period, depending on temperature. At hatching the larvae have a mean length between 3 and 4 mm. Newly hatched larvae have a lower specific gravity than eggs and rise immediately, concentrating in the upper 50 m. Eggs and larvae in Shelikof Strait are often found in distinct patches that can be followed spatially and temporarily for several weeks as they slowly drift southwest with the prevailing currents (Incze et al. 1989, 1990). They remain planktonic at least until July. Very little is known about their juvenile stage.

The study area

The southeast and southcentral coast of Alaska is indented by numerous fjords and larger fjord-like bays. Resurrection Bay is a fjord of approximately 32 km length and 4-8 km width located within the coastal mountain range on Kenai Peninsula (Fig. 1). The fjord's longitudinal bathymetry shows an inner basin with a maximum depth of close to 300 m, separated by a sill from the outer basin (Fig. 2). The sill is located about 15 km from the mouth of the fjord at the narrowest point along the longitudinal axis and it rises to a depth of approximately 185 m. The outer basin is slightly shallower than the inner basin and has an open connection with the shelf.

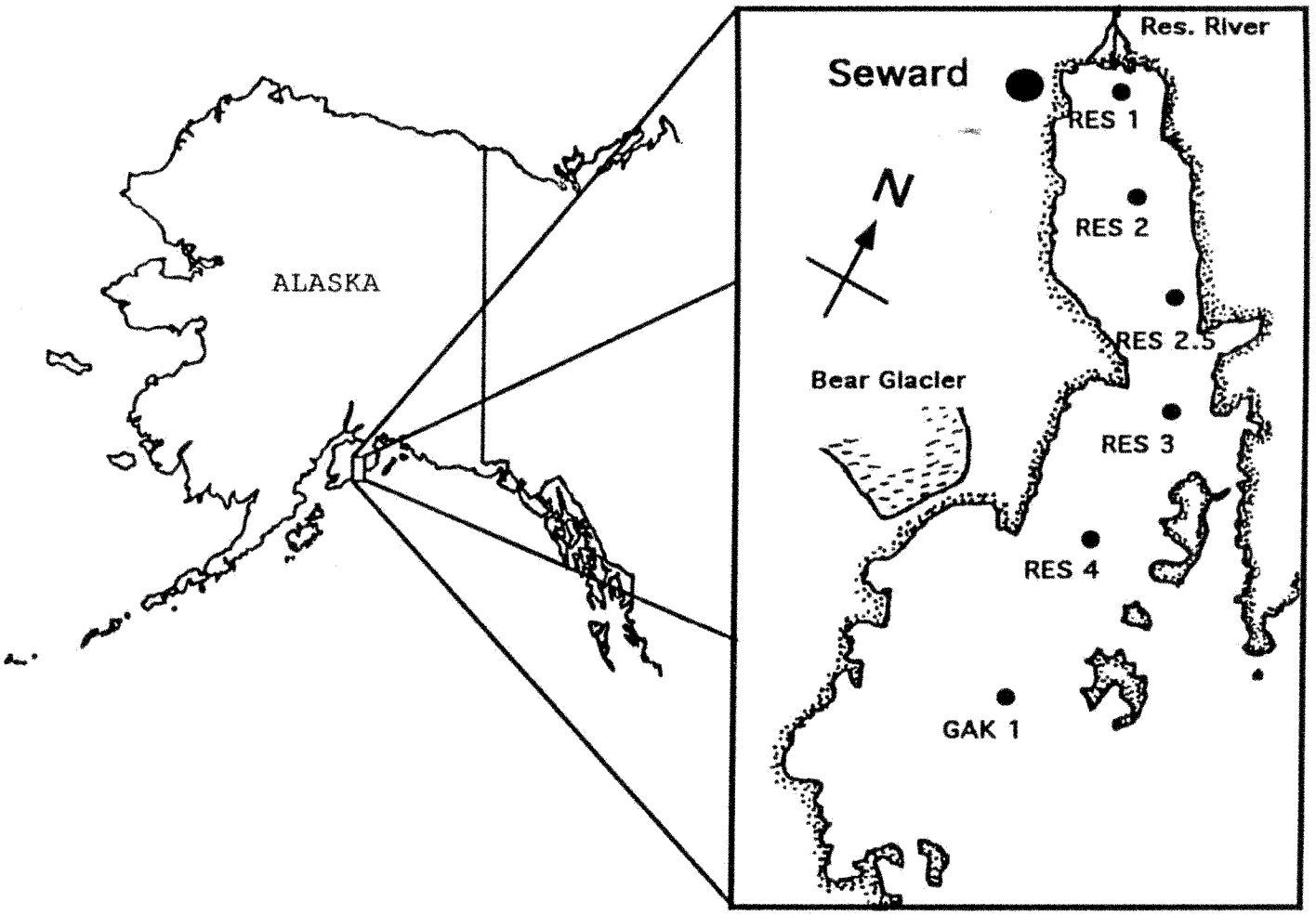


Fig. 1 Map of Alaska and Resurrection Bay showing station locations.

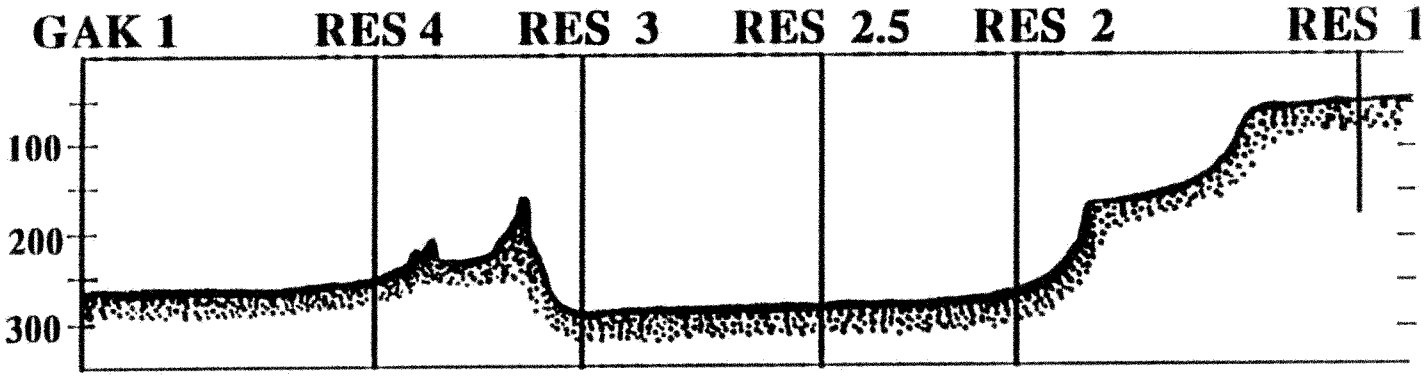


Fig. 2 Longitudinal bathymetry profile of Resurrection Bay, Alaska. Depth in meters.

Resurrection River, a glacial stream, discharges freshwater at the head of the fjord near the town of Seward and numerous other, smaller creeks enter from the mountainous sides. Resurrection River is the principal source of freshwater and has an average discharge rate of 110 $m^3 s^{-1}$ during the peak runoff period. Freshwater discharge is highly seasonal with minimal discharge in late winter and a maximum observed in October. A secondary maximum may occur in May due to melting of the winter snowpack (Royer 1982). Another source of freshwater for Resurrection Bay is Bear Glacier, which discharges meltwater and ice directly into the outer basin of the fjord. Changes in runoff rates result in density changes in the fjord, which, together with density changes on the shelf, determine some of the water exchange processes between Resurrection Bay and the open shelf.

The dominant oceanographic feature on the shelf is the Alaska Coastal Current (ACC), flowing across fjord's mouth in a westward direction. The ACC is a baroclinic coastal current flowing cyclonically around the Gulf of Alaska. Variability in wind stress and freshwater discharge cause variations in the ACC (Johnson et al. 1988). Such variations can cause changes in the free surface elevation and pycnocline depth at the mouth of a fjord, which will influence circulation within the fjord (Klinck et al. 1982). The ACC not only affects circulation within Resurrection Bay but also links fjords along the coast.

In the Gulf of Alaska strong easterly winds dominate from autumn through spring, causing onshore Ekman transport (Johnson et al. 1988). The resulting coastal convergence favors inflow of surface water into Resurrection Bay and outflow of deeper waters. However, these conditions are generally associated with strong

downfjord winds (Royer pers. comm.) that can result in a surface outflow and a convergence at the mouth of the fjord. Throughout summer, easterly wind stress relaxes and possibly reverses. This relaxation and occasional westerly winds cause a divergence along the coast, favoring outflow of surface water onto the shelf and inflow of deep water (Heggie et al. 1977). In summer a high pressure region dominates the gulf, resulting in upfjord winds and posibly inflow at the surface. At present it is not clear whether the inflow/outflow is driven by upwelling/downwelling on the shelf or is more locally controlled by upfjord/downfjord winds, or by other factors. Regardless of the mechanisms involved, events that cause water exchanges between the fjord and the shelf can have a profound influence on the plankton community within the fjord.

Our previous knowledge of the water exchange processes between Resurrection Bay and the shelf are limited to investigations of deep water renewal mechanisms. Heggie et al. (1977), from their observations in Resurrection Bay, concluded that exchange of water takes place below 150 m depth and is limited to the period from May through September, when downwelling conditions are absent from the shelf. Niebauer's (1980) modelling results for Resurrection Bay suggest continuous year-round deep water renewal, driven by coastal upwelling and downwelling on the adjacent shelf.

The hydrographic similarities between the coastal fjords or fjord-like systems (e.g. Prince William Sound) and the Shelikof Strait region, which has been described as an estuarine-like system (Kim 1989), suggest that conditions in areas like Prince William Sound or Resurrection Bay may be as suitable for growth and survival of pollock as those in Shelikof Strait.

Larval growth dynamics

Larval growth rates can vary in time and space as a result of differences in environmental conditions. Houde (1987) has shown that small variations in growth rates and resulting effects on stage duration can cause large fluctuations in recruitment. He concluded that an analysis of growth rate variability in the early life stages can provide important insight into fluctuating recruitment levels. An additional advantage of analyzing growth rates is that they are easier to obtain and more reliable than estimates of other characteristics such as mortality.

Growth rates are linked to environmental conditions in a variety of ways. Hamai et al. (1971) documented temperature dependance of growth rates for larval pollock and Paul (1983) found a relation between feeding success of larval pollock and water temperature. Growth rates are also related to food concentrations (Haldorson et al. 1989a, b) and probably to salinity (Bulatov 1989). Furthermore, growth rate determines the period of time in which the larvae are most susceptible to predation. Miller et al. (1988) have shown that it is generally the smallest size classes that are most vulnerable to predation. Thus a high growth rate can be associated with a reduced loss to predation, while low growth rates are indicative of suboptimal conditions and possibly a lower survival rate. Estimates of larval growth rates can help to identify those environmental parameters that determine survival and will ultimately improve our understanding of the dynamics of fish populations (Fritz et al. 1990).

Growth rates for walleye pollock have been compared between different geographic locations and between years (Walline 1984, Yoklavich and Bailey 1988, 1990, Haldorson et al. 1989a, b). Because

there are only data from one year available for Resurrection Bay, this study will be limited to comparing growth rates within one year between different stations and to other studies.

Distribution of hatch dates and spawning dates help identify the conditions that are required for successful larval survival. If the local water movements are known sufficiently, spawning dates can help to identify possible spawning sites. Conversely, the age distribution at different stations can identify water movements between the fjord and shelf.

Objectives

A literature review suggests that the importance of Alaskan fjords for fishes has not been evaluated, although studies elsewhere indicate that fjords are important for fish production. A widely used approach to clarify the role of environmental factors for successful recruitment is an analysis of the growth dynamics of fish larvae. This study uses growth analysis together with distribution and abundance data to evaluate the role of one fjord in the early life history of walleye pollock. Specifically, the objectives of this study are to:

1. determine distribution and abundance of walleye pollock larvae in Resurrection Bay.
2. quantify growth rates of larval pollock within a fjord with glacial influence and compare growth rates to literature values from other areas.
3. estimate hatch dates and spawning dates of the observed population.
4. analyze length-frequency distributions in relation to station location and water movements.

5. assess the role of Resurrection Bay in the early life history of walleye pollock.

This is the only study to date that examines the early life history of walleye pollock larvae in a glaciated fjord system. The study thus provides the unique opportunity to compare the observed parameters in a glaciated fjord to literature values from other habitat types. These include a shallow, well protected bay in SE-Alaska (Auke Bay); a deep, fjord-like trench without glacial influences (Shelikof Strait); a broad continental shelf (SE Bering Sea); and a large, shallow bay in Japan (Funka Bay). Except for Funka Bay all these areas occur at latitudes similar to Resurrection Bay.

MATERIALS AND METHODS

Biological Data

Field Collection

Ichthyoplankton samples for this study were collected from the *R/V Little Dipper*, a 28 ft. aluminum boat, during two cruises in 1989. Sampling dates were 1-4 May 1989 (LO001) and 7-9 June 1989 (LO002). During both cruises 6 stations were sampled along the fjord axis (Fig. 1).

Horizontal plankton tows were taken at discrete depths or over small depth increments if the vertical position of the net changed during tows. The gear used to sample was a 1 m^2 National Institute of Oceanography tucker trawl, rigged with two 505μ mesh nets. A drogue net was open while the trawl was lowered to the desired depth. The drogue net served to stabilize the frame and prevent sudden depth changes as a result of opening the second net. The nets were rigged to a double tripper which allowed the second net to be opened and closed via messenger from the surface. The net was generally towed for 5 minutes in the direction of the tidal flow. Towing speed was between 1.5 and 2.5 knots, the slowest possible speed of the *R/V Little Dipper*. A TSK or GO flowmeter was attached in a central position in the mouth of the net. Volumes filtered were calculated from flowmeter readings.

All samples were immediately preserved in 50% Isopropyl alcohol, 90% Ethyl alcohol or 10% formalin. The alcohol was renewed twice on each sample after 24 hours and after 2-3 days. Tables 1 and 2 list all samples, their depths, and the number of walleye pollock captured for LO001 and LO002.

In conjunction with most tows a Seabird Seacat Profiler (SBE

Table 1: Ichthyoplankton samples collected in Resurrection Bay during LO001, 1-4 May, 1989. Numbers in parentheses include disintegrated larvae assumed to be walleye pollock. ISO = isopropyl alcohol, EtOH = ethyl alcohol. * = volume filtered was estimated from similar net tows.

station	depth	number of larvae		volume (m^3)		larval density (number m^{-3})		preserved in
RES 1	13	188	(201)	127.8		1.09	(1.16)	ISO
	25-28	303	(318)	147.3		2.12	(2.22)	EtOH
5/4/89	39	91	(99)	144.6		.63	(.68)	ISO
	68	5	(6)	124.7		.04		ISO
	105	6		95.9		.06		ISO
RES 2	7	481	(577)	209.3		2.30	(2.76)	ISO
	30	1327	(1461)	159.0	*	8.35	(9.19)	EtOH
5/4/89	60	24	(25)	134.1		.18		ISO
	150	21	(23)	134.4		.04		ISO
	260-285	8	(10)	159.0		.06		ISO
RES 2.5	19	1128	(1133)	260.9		4.32	(4.34)	ISO/EtOH
	30	546	(582)	263.0	*	2.08	(2.21)	EtOH
5/3/89	48	490	(520)	263.0	*	1.86	(1.98)	EtOH
	70	45	(47)	273.0		.17		EtOH
	90-110	36	(38)	306.4		.12		ISO
	140-180	35	(36)	226.5		.16		EtOH
	200-230	40	(41)	335.6		.12		ISO
	0-250	448	(464)	388.6		1.15		EtOH
RES 3	18	919	(1869)	359.3		2.56	(5.20)	ISO
	55-62	95	(98)	261.2		.36	(.38)	ISO
5/3/89	100	13		240.8		.05		ISO
	150	19	(21)	269.8		.07		ISO
RES 4	18	1618	(1869)	238.9		6.77	(7.34)	ISO/EtOH
	26	1490	(1492)	135.2		11.02	(11.92)	EtOH
5/2/89	37	437	(932)	229.8		1.90	(4.06)	EtOH
	66	735	(781)	155.1		4.74	(5.04)	ISO
	105	6		196.2		.03		EtOH
	140-165	15	(17)	194.0	*	.08		EtOH
	150-170	11	(15)	208.3		.05		EtOH
	190-215	13		194.0		.07		EtOH
	250-270	23		184.3		.18		EtOH

Table 1: continued

station	depth	number of larvae	volume (m^3)	larval density (number m^{-3})	preserved in
GAK 1	22	983 (1266)	277.3	3.54 (4.57)	ISO
	32	320 (1204)	255.3	1.25 (4.72)	ISO
5/1/89	65	2534 (2832)	240.2	10.55 (11.79)	ISO
	100	29 (30)	212.3	.14	ISO
	105-115	11 (15)	205.0	.05	ISO
	150-170	24 (29)	207.5	.11	ISO
	200-225	24 (26)	270.1	.09	ISO
	250-280	30	157.7	.19	ISO

Table 2: Ichthyoplankton samples collected in Resurrection Bay during LO002, 7-9 June, 1989. ISO = isopropyl alcohol. * = volume filtered was estimated from similar net tows. ** = depth was estimated from wire angle and length of wire out.

station	depth (m)	number of larvae	volume (m^3)	larval density (number/m^3)	preserved in
RES 1	10	7	280.6	2.49	ISO
	14	2	287.0	.70	"
6/8/89	24	2	243.7	.82	"
	35	2	279.5	.72	"
	62	0	241.6	.0	"
	75	0	206.1	.0	"
RES 2	11	21	237.8	8.83	ISO
	22	8	231.6	3.45	"
6/9/89	33	29	236.2	12.28	"
	55-65	2	228.7	.87	"
	95-105	0	255.0	.0	"
	140-160	0	303.9	.0	"
RES 2.5	5	2	310.4	.64	ISO
	12	7	241.1	2.90	"
6/8/89	25	13	261.7	4.97	"
	44	9	296.7	3.03	"
	65	1	247.5	.40	"
	86	0	227.6	.0	"
	104-112	0	216.6	.0	"
	150 **	0	238.6	.0	"
	200 **	0	272.2	.0	"
	250 **	0	318.7	.0	"
RES 3	12	17	246.4	6.90	ISO
	22	4	239.7	1.87	"
6/8/89	38	21	308.8	6.80	"
	58	92	232 *	39.66	"
	70-82	6	232 *	2.59	"
	100 **	0	249.9	.0	"
	150 **	0	265.5	.0	"

Table 2: continued

station	depth (m)	number of larvae	volume (m^3)	larval density (number/100m^3)	preserved in
RES 4	11	5	260.9	1.92	ISO
	22	6	256.1	2.34	"
6/9/89	29	6	253.7	2.36	"
	45	28	200.7	13.95	"
	70	19	260.9	7.28	"
	84-98	0	464.6	.0	"
	135-155	0	383.5	.0	"
	174-192	0	286.2	.0	"
GAK 1	16	78	249.1	31.14	ISO
	25	8	254.5	3.14	"
6/7/89	35	25	246.7	10.13	"
	57	0	232.2	.0	"
	63	0	309.8	.0	"
	160-185	0	210.4	.0	"
	195-220	0	225.7	.0	"
	245-260	0	316.8	.0	"

19) was attached to the net to record conductivity, temperature and pressure throughout the tow. These records were used to obtain actual depths of the net. When no CTD data were recorded, depth was estimated from the wire angle and the length of wire out.

All samples were sorted in the laboratory to isolate finfish eggs and larvae from zooplankton. Walleye pollock larvae were separated and their standard length measured. A BioQuant image analysis system, including a high resolution video system and a digitizer, allowed identification, measurement, and data entry all in one step.

Abundance estimates

Abundance at each station was estimated by integrating larval densities over the water column, using vertical distribution profiles. Density was assumed to be zero at the surface and to change in a linear fashion between successive sampling depths. Confidence limits could not be calculated, because no replicates were taken.

Larval size

Estimates of larval size are easily obtained by measuring standard length (SL). Standard statistical procedures (see below) were used to compare larval length from the same samples preserved in different preservatives, from samples at the same station at different depths and from samples at different stations.

The effect of preservatives on measured standard length was examined using two samples that were each split into two subsamples. The subsamples were preserved in isopropyl alcohol and ethyl alcohol and their mean lengths were compared. Since the results suggested differences between the two means I used only samples that were preserved in the same preservative in all subsequent statistical tests.

The relation between size and vertical distribution was

examined at all stations by comparing SL of larvae from all samples collected at a station.

The size differences between stations were examined using only the shallowest samples from each station that were preserved in the same preservative, thus minimizing errors resulting from differences in size due to preservation and vertical distribution. In addition, samples from all depths were pooled for each station and the mean of the pooled data was compared between stations for each preservative. For between station comparisons, larval mean SL was corrected for the date of sampling using growth rates obtained during this study.

Samples from stations deeper than 100 m were not included in the analysis since numbers of larvae were low and contamination of the net while retrieving it cannot be excluded.

Aging and growth rate determination

Otolith increment deposition has been shown to be daily for larval and juvenile walleye pollock to at least 100 days. A well defined increment is deposited at hatching (Nishimura and Yamada 1984, Bailey and Stehr 1988). Bailey and Stehr (1988) validated daily deposition for otoliths from walleye pollock larvae that were reared under optimal and suboptimal conditions in the laboratory. They found 3-4 pre-hatching increments, but the hatching increment was clearly distinguished. The resolution of daily increments was only disrupted after four days of starvation. The otolith increment technique is a reliable and well established technique for aging larval walleye pollock.

Ages of larvae were estimated from the number of increments on sagittal otoliths. Otoliths were removed under a dissecting microscope using a pair of fine needles. The microscope was fitted with polarizing filters to enhance visibility of otoliths. Whole otoliths

were mounted on micro slides with clear mounting medium. Increments were counted on both sagittae under a compound microscope at 1000x magnification using a high resolution video screen to view the otoliths. Increments were independently counted a second time by the same reader. Readings were confirmed for a subsample of 20 otoliths by a NOAA/NMFS/AFSC (Seattle) laboratory. Only those independent readings that did not differ by more than one increment, in which case the higher count was used, were used for growth determination.

Random subsamples of larvae from two stations, one in the inner basin (RES 2) and one in the outer basin (RES 4) were examined for age determination. In random subsamples the number of larvae from each length category is theoretically proportional to the total number in that length category. Random sampling has been found to be superior to fixed-age subsamples, in which a constant number of larvae from each length interval is aged (Kimura 1977).

Larval growth rates were determined by fitting linear regression lines to length at age data. Spawning dates were estimated after accounting for temperature dependent egg stage duration. No data are available for distribution of eggs spawned in the vicinity of Resurrection Bay, but eggs are generally found below 150 m in Shelikof Strait (Kendall and Kim 1989). Assuming a distribution similar to that in Shelikof Strait, incubation temperatures were estimated from temperature profiles obtained at RES 2 and GAK 1 during a cruise on April 6, 1989. Incubation temperature was estimated as the mean temperature between 150 m and the bottom. Egg stage duration was then calculated using equations derived by Haynes and Ignell (1983) that relate temperature and incubation period for walleye pollock.

Physical Data

Using a portable CTD, Seabird SBE 19 Profiler, hydrographic data were taken at each station and along six cross-fjord transects through the stations during May. Salinity, temperature, and density profiles were plotted for each station and for transects across each station for early May 1989. Additional CTD-profiles for RES 2.5 and GAK 1 were plotted from data collected during a cruise on April 6 of the same year to examine water characteristics prior to sampling.

To obtain a point measurement of currents across the sill two Aanderra current meters were moored just outside the sill on June 9, 1989. The current meters were moored at 15 m and 200 m depth just seaward of the sill, approximately one mile south of RES 3. Current speed and direction as well as conductivity and temperature were measured every 4 hours for 135 days until the mooring was retrieved on October 23, 1989.

In addition, CTD data from RES 2.5 and GAK 1 that were obtained over the past 20 years during transects of research vessels through Resurrection Bay, were reviewed to describe some general circulation features. ADCP transects through Resurrection Bay and from the "Cape Fairfield" line were also reviewed (For dates see Table 3 and Fig. 21). The Cape Fairfield line is located just upstream of Resurrection Bay along 148.8° N and transects the ACC from the coast to approximately 50 km offshore (Fig. 3). The ADCP transects were obtained during several cruises of the *R/V Alpha Helix* between March 1986 and October 1990.

Statistical procedures

For all size comparisons, standard statistical tests as implemented in SYSTAT (Wilkinson 1990) were used. For all two-sample

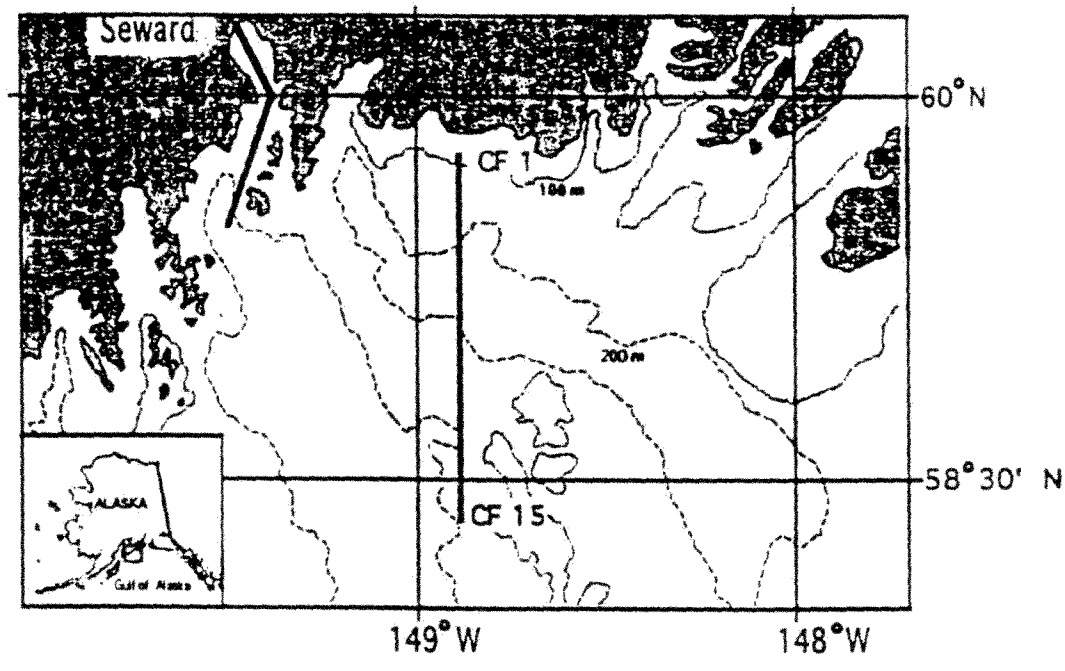


Fig. 3 ADCP transect lines along the Resurrection Bay and Cape Fairfield lines in the Gulf of Alaska.

comparisons a Student t-test was used. To detect differences in mean standard length of larvae between multiple samples a one-way ANOVA was used. A Tukey multiple comparison test was employed to determine between which means the equalities or inequalities lie (Zar 1984).

These parametric tests assume that the variable is normally distributed and that variances are equal, but they are robust to considerable deviations from these assumptions (Zar 1984). Since a test for normality (Zar 1984) and a Bartlett test for homogeneity showed that both of these underlying assumptions were sometimes violated in my samples, nonparametric tests were employed in addition to parametric test procedures in these cases.

The nonparametric test procedures employed were a Kruskal-Wallis test (nonparametric analysis of variance), a Mann-Whitney test for two sample comparisons, and a Tukey-type multiple comparison test (Zar 1984). Results of the multiple comparison tests are only presented where they differ from those obtained using parametric test procedures.

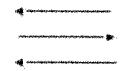
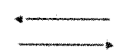
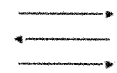
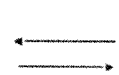
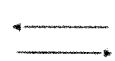
The linear regression equations describing growth were compared between stations to test for differences in regression coefficients. Slopes and elevations were compared using Student's t-statistic as described in Zar (1984).

RESULTS

General circulation

Several 'snap-shots' of the current profile in Resurrection Bay obtained from ADCP transects show no consistent vertical current structure. Flow can be upfjord at the surface on both flooding and ebbing tides (Table 3 and Fig. 4). On several occasions a three-layered flow was observed with either upfjord flow at the surface and near the bottom and down-fjord flow at intermediate depth or vice versa. Fig. 4 shows several examples of these observed current profiles. Table 3 also lists the upwelling indices at 60° N, 149° W for 4 days prior to and on the day the ADCP transects were taken. There is no consistent relationship between the upwelling indices and the flow patterns in the fjord. For the few dates with ADCP data, four sampling dates were preceded by a period of steady down-welling. After two of these periods (4/4/88, 11/29/88) surface flow was upfjord, as may be expected for downwelling conditions. After the other two downwelling periods (3/17/87, 11/30/87) surface flow was downfjord. In four other cases downwelling conditions were giving way to upwelling conditions just prior to or on the day of sampling. On 1/5/86, 4/18/88 and 12/12/88 relaxation of downwelling was followed by an outflow of surface water on both flooding or ebbing tides. Only on 9/29/88, during maximum flood tide, was the relaxation in downwelling followed by surface inflow. A period of weak upwelling that changed to weak downwelling on the day of sampling (5/26/87) was followed by upfjord flow at the surface during a slacking flood tide. On 6/29/88 there was neither strong up- nor downwelling prior to sampling. Surface flow was upfjord at maximum flood tide.

Table 3: Direction of flow at the surface, at intermediate depth, and near the bottom obtained from ADCP profiles in Resurrection Bay. Upwelling indices four days prior to (-4 to -1) and on the day of sampling (0) at 60 N, 149 W.

date	time (ADT)	tide	flow pattern downfjord ←→ upfjord	upwelling index -4	-3	-2	-1	0
1/05/86	21:15	flood tide		-153	-111	-45	-7	11
03/17/87	23:40	max. flood tide		-40	-48	-45	-28	-13
05/26/87	12:40	slacking flood tide		12	12	-3	12	-17
11/30/87	13:15	max. ebb tide		0	-100	2	-25	-23
04/04/88	11:30	slacking ebb tide		-38	-43	-31	-65	-62
04/18/88	10:50	slacking ebb tide		-70	-226	-48	-14	19
06/29/88	12:20	max. flood tide		-8	1	4	1	-4
09/29/88	02:50	max. flood tide		-53	-14	-111	-144	-1
11/29/88	11:40	mid ebb tide		-27	-236	-56	-116	-132
12/12/88	15:40	mid flood tide		-125	-88	-166	-92	17

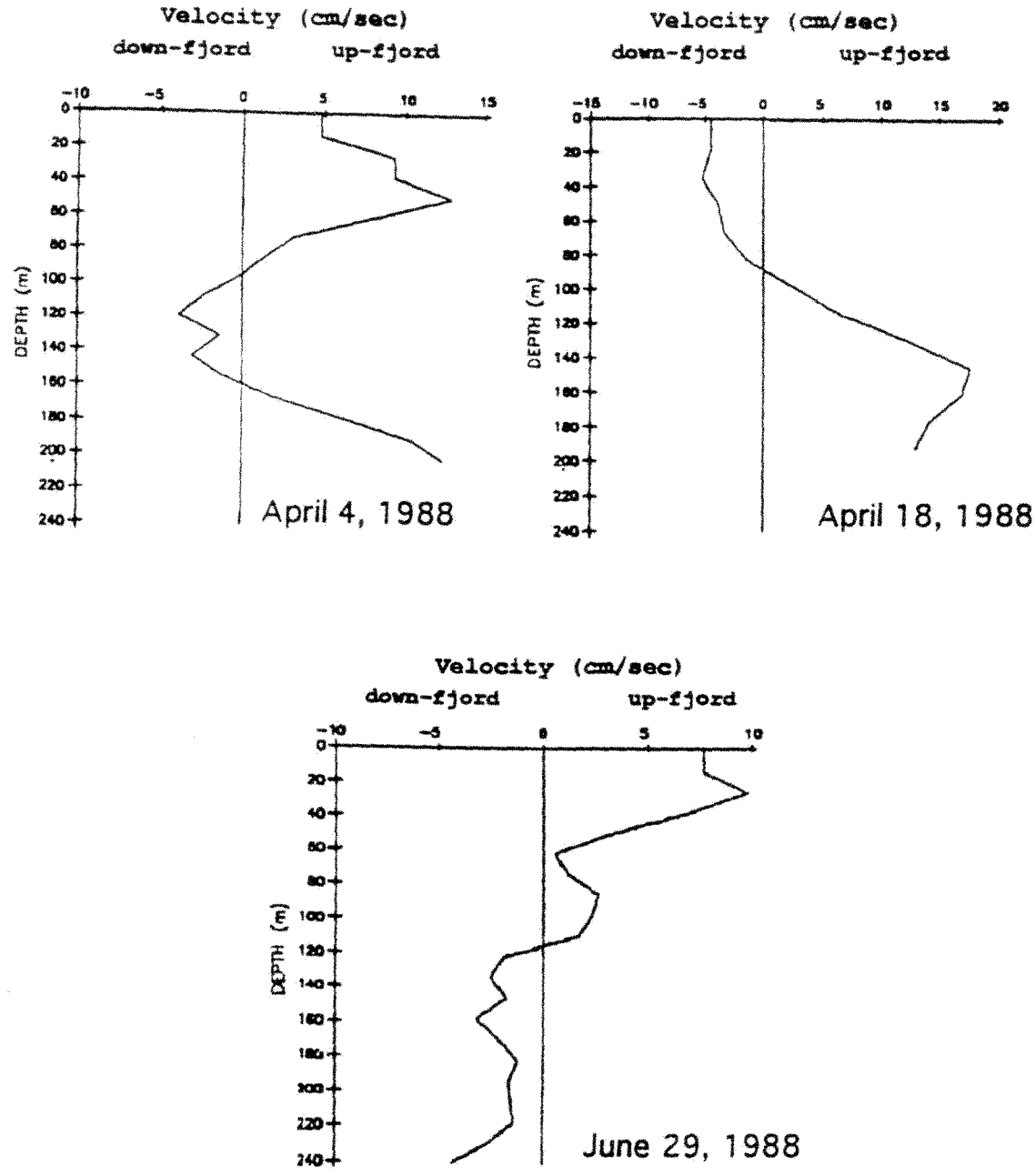


Fig. 4 Vertical current structure in Resurrection Bay on three different days in the spring and summer of 1988. Shown is the North-South component of flow, averaged along the transect line. For tidal phase and upwelling indices at the time of sampling see Table 3.

Hydrographic observations during 1989

On April 6, 1989, temperatures at RES 2.5 and GAK 1 increased with depth from approximately 4°C in the surface layer to almost 6°C below 200 m (Fig. 5). The upper 100 m, above the permanent thermocline, were nearly homogenous with a slightly higher temperature in the upper 10 m. The elevated temperature above 10 m indicates that a seasonal thermocline was starting to develop. Temperatures above the permanent thermocline (> 100 m) are about 0.5°C lower inside the fjord (RES 2.5) than near its mouth (GAK 1).

Salinities in April increased from 31.7 psu at the surface to 33.3 psu near the bottom at GAK 1 in the outer basin (Fig. 6). For the upper 180 m salinities at RES 2.5 were virtually identical to GAK 1, except for a shallow lens of slightly fresher water at the surface at RES 2.5 due to river runoff or precipitation. The salinity was reduced by only approximately 0.2 psu, indicating that freshwater discharge is small at this time of year. Below 180 m, corresponding to the sill depth, salinity profiles differed in the two basins.

The density profiles in April (not shown) closely follow those of salinity (Fig. 6), since densities at high latitudes (low temperatures) are primarily driven by salinity, rather than temperature. Like salinity, the density below sill level differed between the inside and outside station because the free exchange of water masses below sill level is restricted. At sill level, the water at GAK 1 was more dense than at RES 2.5, while at greater depths density was lower at GAK 1.

Between April and May 1989 the water properties of the water masses inside and outside the fjord changed considerably. A strong seasonal thermocline had developed near 20 m at RES 1 and near 10 m

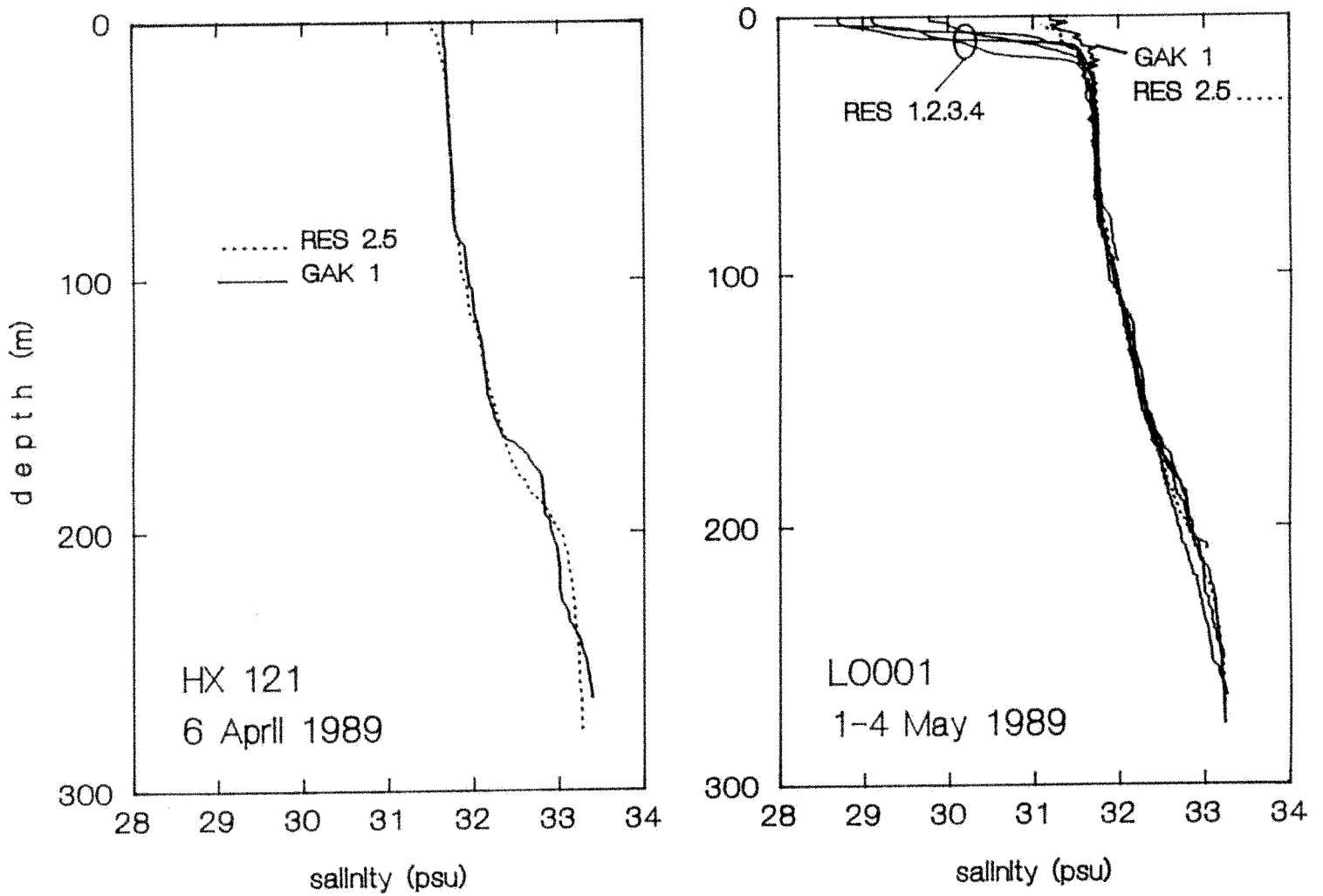


Fig. 5 Temperature profiles at six stations in Resurrection Bay, Alaska, early April and early May 1989.

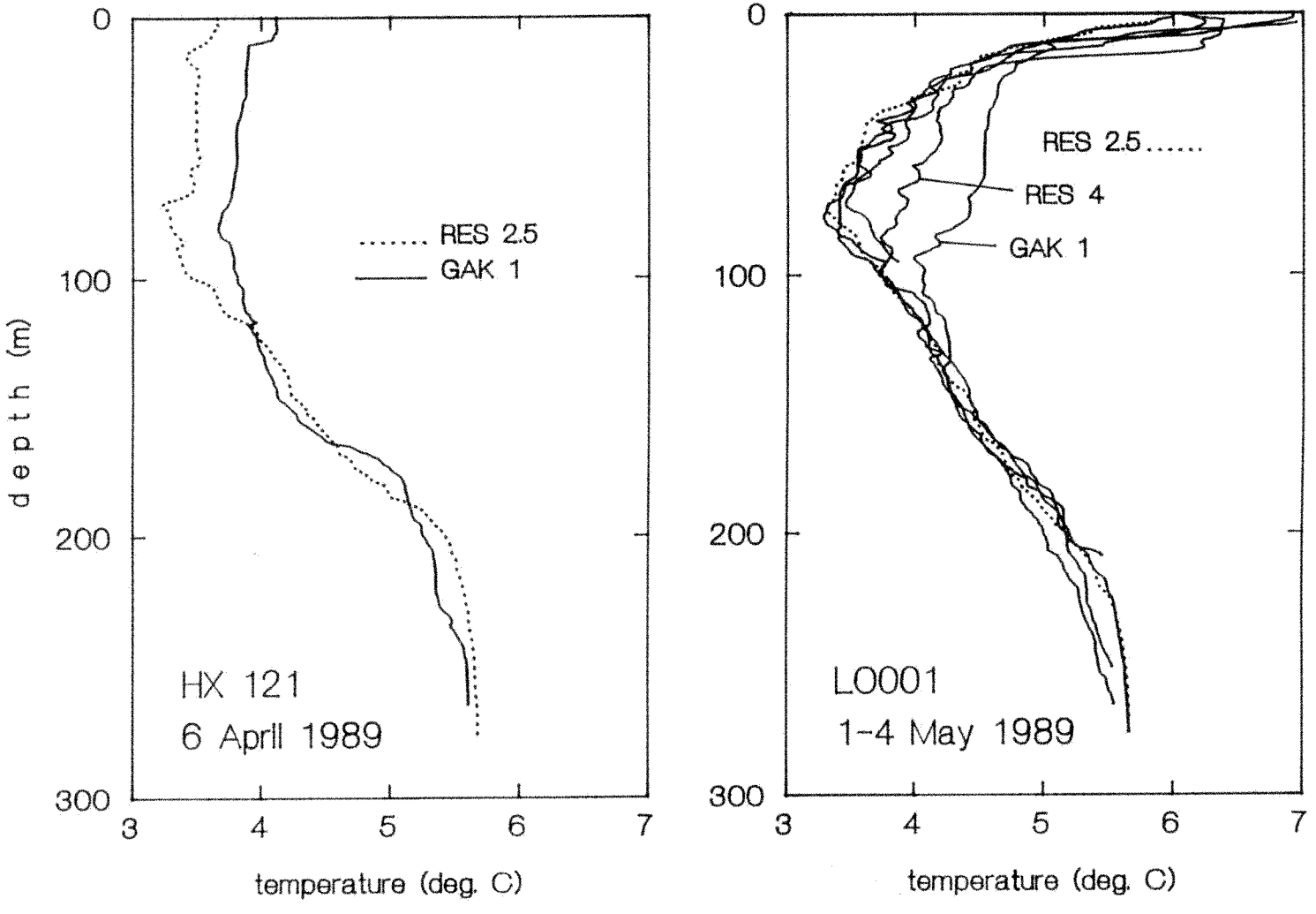


Fig. 6 Salinity profiles at six stations in Resurrection Bay, Alaska, early April and early May 1989.

at all other stations. The surface temperature varied between 5.8°C at RES 2.5 and 7°C at RES 3 (Fig. 5). All temperature profiles at the inner stations (RES 1, 2, 2.5, 3) showed a pronounced temperature minimum of about 3.5°C near 80 m. At the outer stations (RES 4, GAK 1) the minimum was somewhat deeper, near 100 m, and the temperature at the minimum was approximately 4°C. The temperature minimum is also obvious in the cross-fjord transects (Fig. 7).

While April temperatures in the upper 100 m did not differ by more than 0.5°C between RES 2.5 and GAK 1, the temperature difference in May was almost 1.5°C. The other inside stations which were sampled in May showed values similar to those at RES 2.5. Temperatures at RES 4, located between GAK 1 and the sill, were intermediate between those at GAK 1 and those inside the sill.

Temperatures at RES 2.5 below about 60 m did not increase between April and May. Thus the temperature minimum of 3.3°C at 80 m was still present at RES 2.5 as well as at the other inside stations. At GAK 1, the temperature minimum at intermediate depth also remained, but it was approximately 0.4°C warmer than in April.

Salinity profiles show a well developed low salinity surface layer at four stations due to river runoff and melting of the snow pack (Fig. 6, Fig. 8). The surface salinities were 2 to 4 psu lower than in April. However, at RES 2.5 and GAK 1 the freshwater lens was much less developed than at the other stations. The surface layer salinity was above 31 psu and almost identical at both stations. Below the halocline salinities were very similar at all stations.

Fig. 9 shows the north-south (V) and east-west (U) components of the current velocity at 15 m depth observed between June 9 and October 23, 1989. The current measurements were filtered to remove variations of the flow with a period less than 35 hours. The

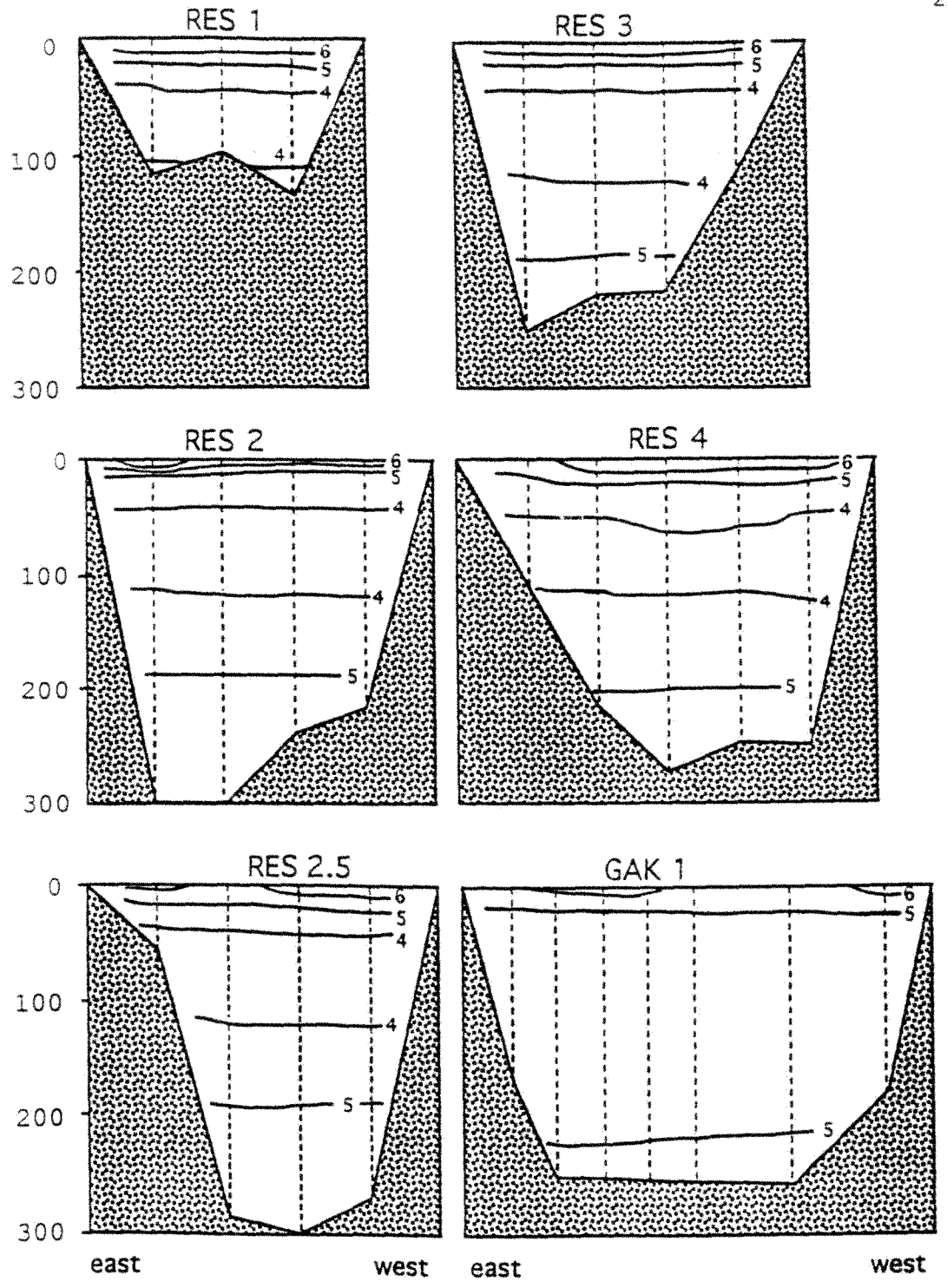


Fig. 7 Cross-fjord transects of temperature across six stations in Resurrection Bay, Alaska 1-4 May 1989. Vertical lines indicate CTD station positions.

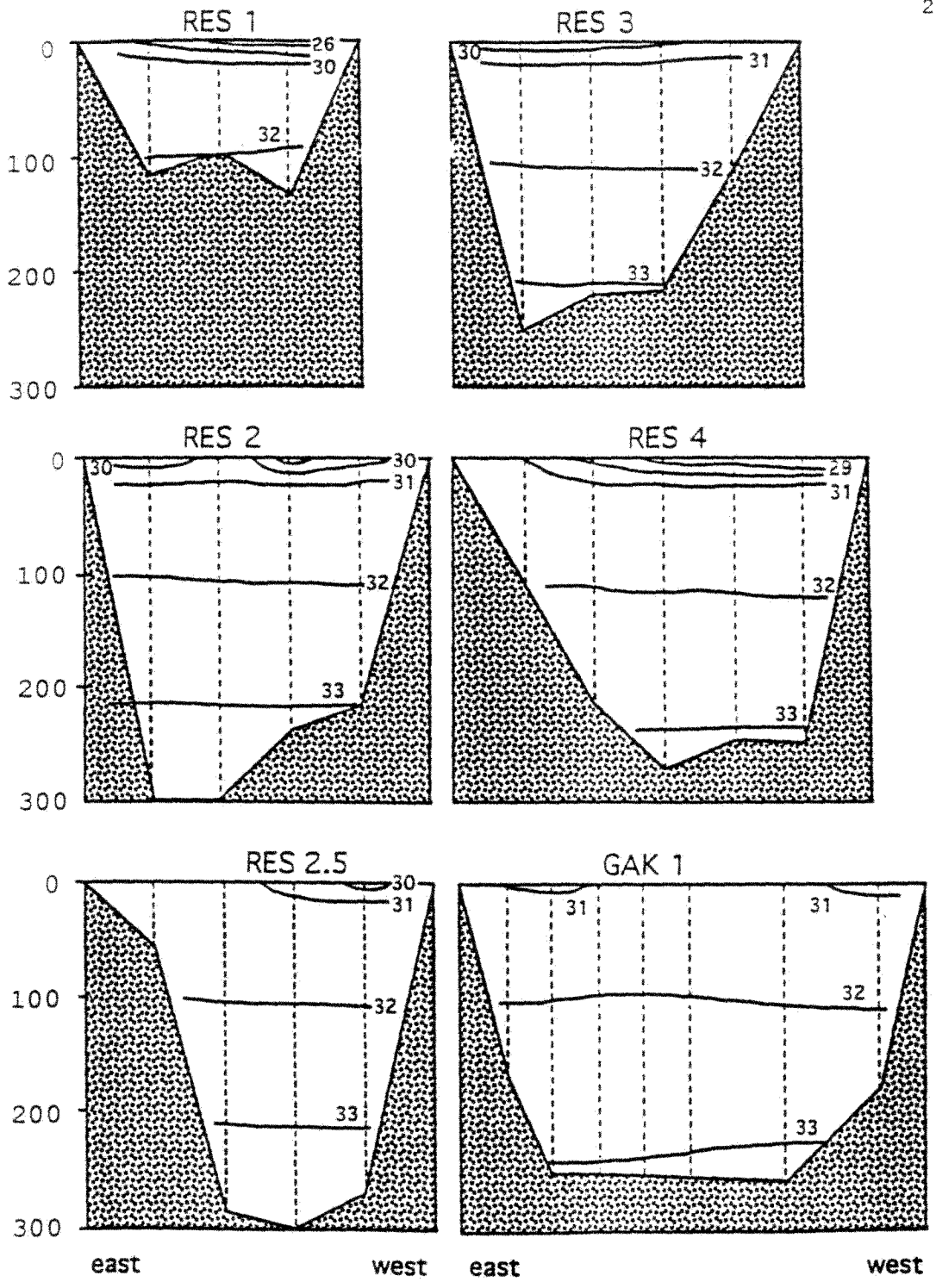


Fig. 8 Cross-fjord transects of salinity across six stations in Resurrection Bay, Alaska, 1-4 May 1989. Vertical lines indicate CTD station positions.

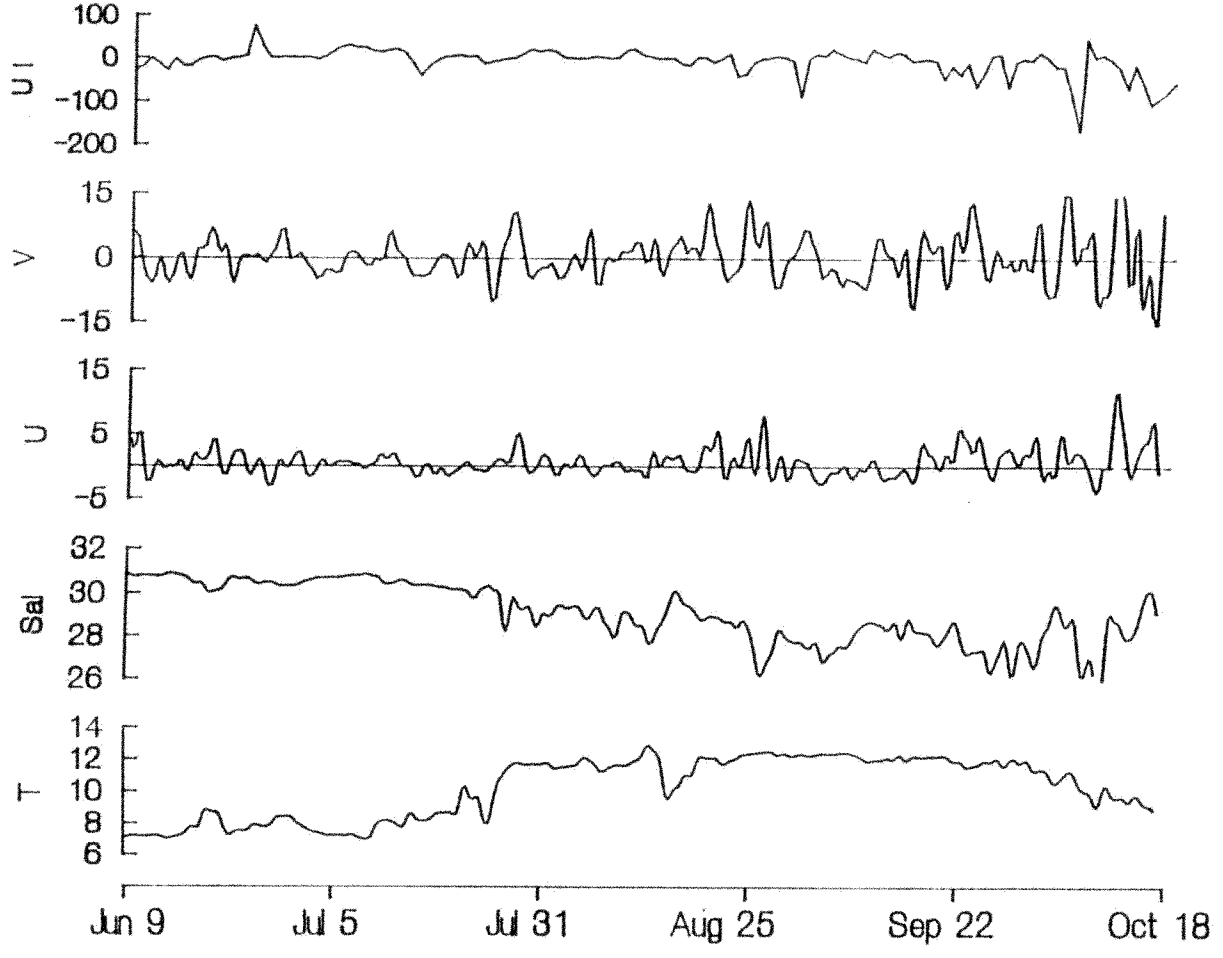


Fig. 9 Current meter data from a 15 m deep station above the sill in Resurrection Bay, Alaska, and Upwelling Index at 60° N, 149° W (UI); 9 June - 22 October 1989. North-south (V) and east-west (U) components of flow (cm/sec), Salinity (psu), and Temperature (C).

resulting north-south component, representing flow along the fjord's axis, varied from -15 cm/sec (southward) to >15 cm/sec (northward) with frequent flow reversals. The overall mean flow, averaged over the period of deployment, was up-fjord at 0.19 cm/sec. Superimposed on the mean flow were fluctuations with a period of about 2-10 days. An analysis of spectral density showed major peaks at diurnal and semidiurnal frequencies corresponding to tides. In addition a significant peak occurred at frequencies of about 0.15 day^{-1} (T. Weingartner, unpubl. data), corresponding to a 7-day period. Fluctuations of a similar frequency are also obvious in the upwelling indices for the same time period (Fig. 9), but a clear relationship between upwelling/downwelling events and the surface inflow and outflow across the sill is not apparent.

Effect of preservatives on length measurements

The different preservatives used strongly affected larval length. Larvae in isopropyl alcohol seemed generally more brittle and shrunk than larvae in either ethyl alcohol or formalin. Two samples were randomly split in half immediately after collection and preserved in isopropyl alcohol and ethyl alcohol for comparison.

Both a student t-test and a nonparametric Mann-Whitney U-test showed highly significant differences in mean SL ($p<0.001$) between larvae in ethyl alcohol and larvae in isopropyl alcohol from both samples that were split ($t=5.050$, $U=57207.5$, $N=1128$ and $t=18.805$, $U=139218.5$, $N=1618$). There was also a highly significant difference in mean SL between larvae in isopropyl alcohol and ethyl alcohol when all samples taken during LO001 were combined by preservative ($t=21.7$; $p<0.005$, $N=14079$). Since most of the samples preserved in ethyl alcohol were collected in the outer basin the differences in

mean SL could in part be due to differences between stations rather than differences between preservatives.

To clarify the effects of preservation I obtained several samples of walleye pollock larvae from Resurrection Bay in the spring of 1991. A sample of about 150 walleye pollock larvae was immediately shipped to Fairbanks for measurements. Unfortunately, all larvae died during the transport. Thus I could only examine the effect of preservatives on larvae that died before preservation. It is possible that they experienced significant shrinkage as a result of death before being preserved. Radtke (1989) found that newly hatched cod larvae shrank from 30 to 40% within 15 min after death.

After preservation of the dead larvae in formalin, ethyl alcohol, 70% isopropyl alcohol, and 100% isopropyl alcohol considerable shrinkage occurred (Fig. 10). In all cases virtually all of the shrinkage occurred within two days after preservation. Maximum shrinkage was observed in isopropyl alcohol and the least amount of shrinkage resulted from preservation in formalin. Larvae shrank an average of 34% in 100% isopropyl alcohol (n=22), 20 % in 70% isopropyl alcohol (n=33), 14% in ethyl alcohol (n=34), and 8% in formalin (n=33) after 2 days of preservation. I concluded that the amount of shrinkage differs between preservatives and subsequently all statistical comparisons were done between samples from the same preservatives.

Distribution and abundance

Vertical distribution

In early May walleye pollock larvae were caught at all stations and at all depths sampled (Table 1). A total of 14,135 larvae from 39 tows were positively identified as walleye pollock larvae.

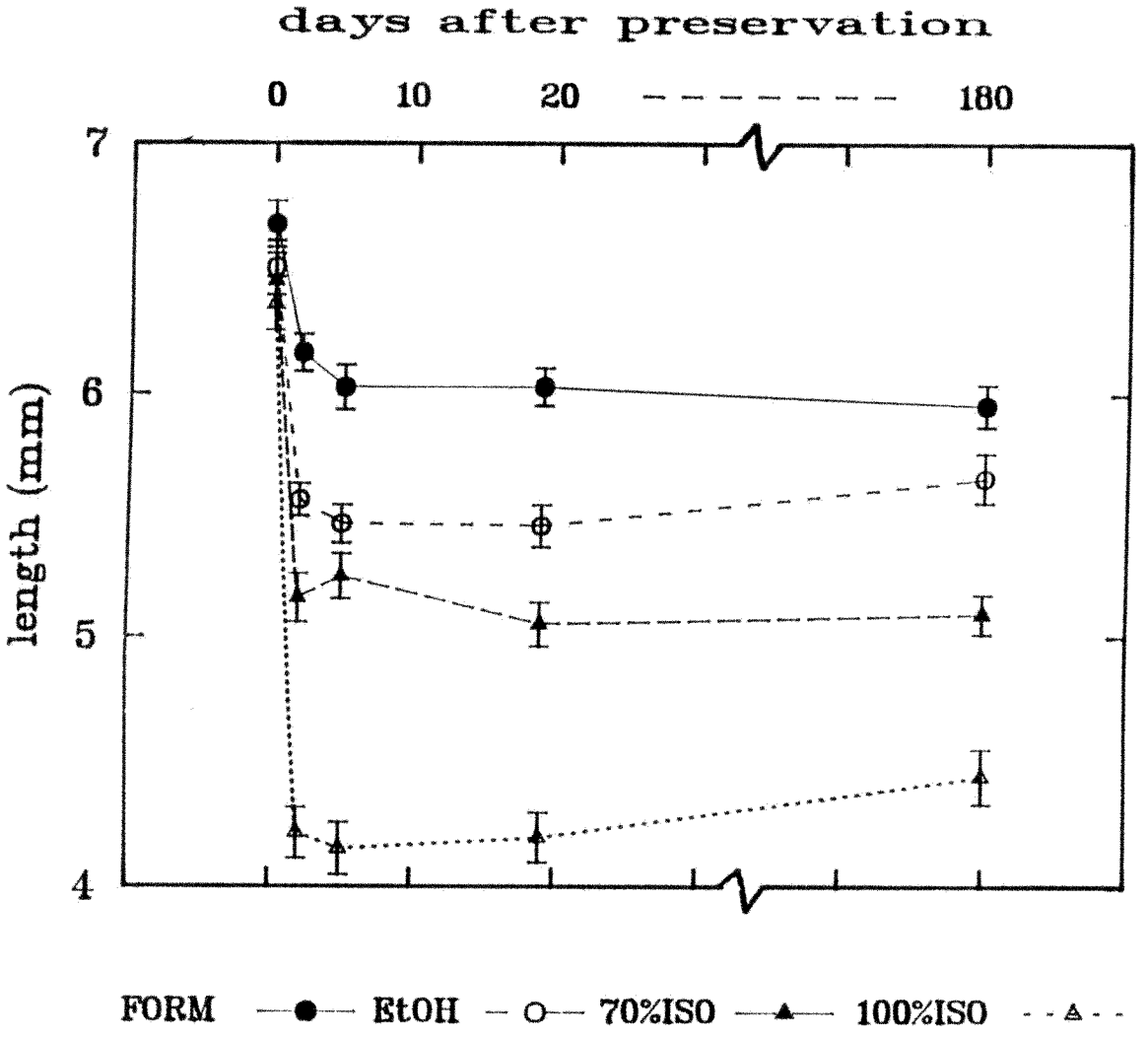


Fig.10 Shrinkage of larval walleye pollock in different preservatives over time. Measurements were made on days 0, 2, 5 ,19, and 180 after preservation.

An additional 2,815 larvae could not be clearly identified, because they were partially disintegrated due to capture and handling. Ninety-eight percent of all larvae that could be identified were larvae of walleye pollock. Thus 98% of the disintegrated larvae were assumed to be walleye pollock for density and abundance estimates. Larval densities ranged from 0.03 larvae m^{-3} (RES 4, 105 m) to a maximum of 11.92 larvae m^{-3} (RES 4, 26 m).

Larvae were generally concentrated in the upper 70 m (Table 1, Fig. 11). Maximum densities occurred at depths between 18 and 30 m at all stations except GAK 1 and ranged from 2.22 larvae m^{-3} to 11.92 larvae m^{-3}. At GAK 1 the maximum in larval density (11.79 larvae m^{-3}) was observed at 65 m. Only one sample was taken in the upper 10 m (RES 2), where larval density was moderately high at 2 larvae m^{-3}. However, density was much higher at 30 m at the same station (9.19 larvae m^{-3}), indicating a subsurface maximum for larval density. At three other stations (RES 1, RES 4, and GAK 1) larval density also had a maximum at intermediate depth, while the shallowest samples had relatively low densities. RES 4 and GAK 1 were the only stations with high observed larval densities below 50 m. Thus, the vertical distribution of walleye pollock in Resurrection Bay shows that larval densities were low at the surface and increased towards depths between 15 and 35 m. Furthermore, larvae were distributed deeper in the water column outside the sill, at stations RES 4 and GAK 1, than at stations inside the sill.

Between May and June larval densities decreased by approximately two orders of magnitude. In early June density ranged from 0 to 0.40 larvae/m^3 (Table 2, Fig. 12). A total of 420 walleye pollock larvae were captured in 45 tows between 5 and 250 m depth. Only tows shallower than 75 m caught pollock larvae. The maxima in larval

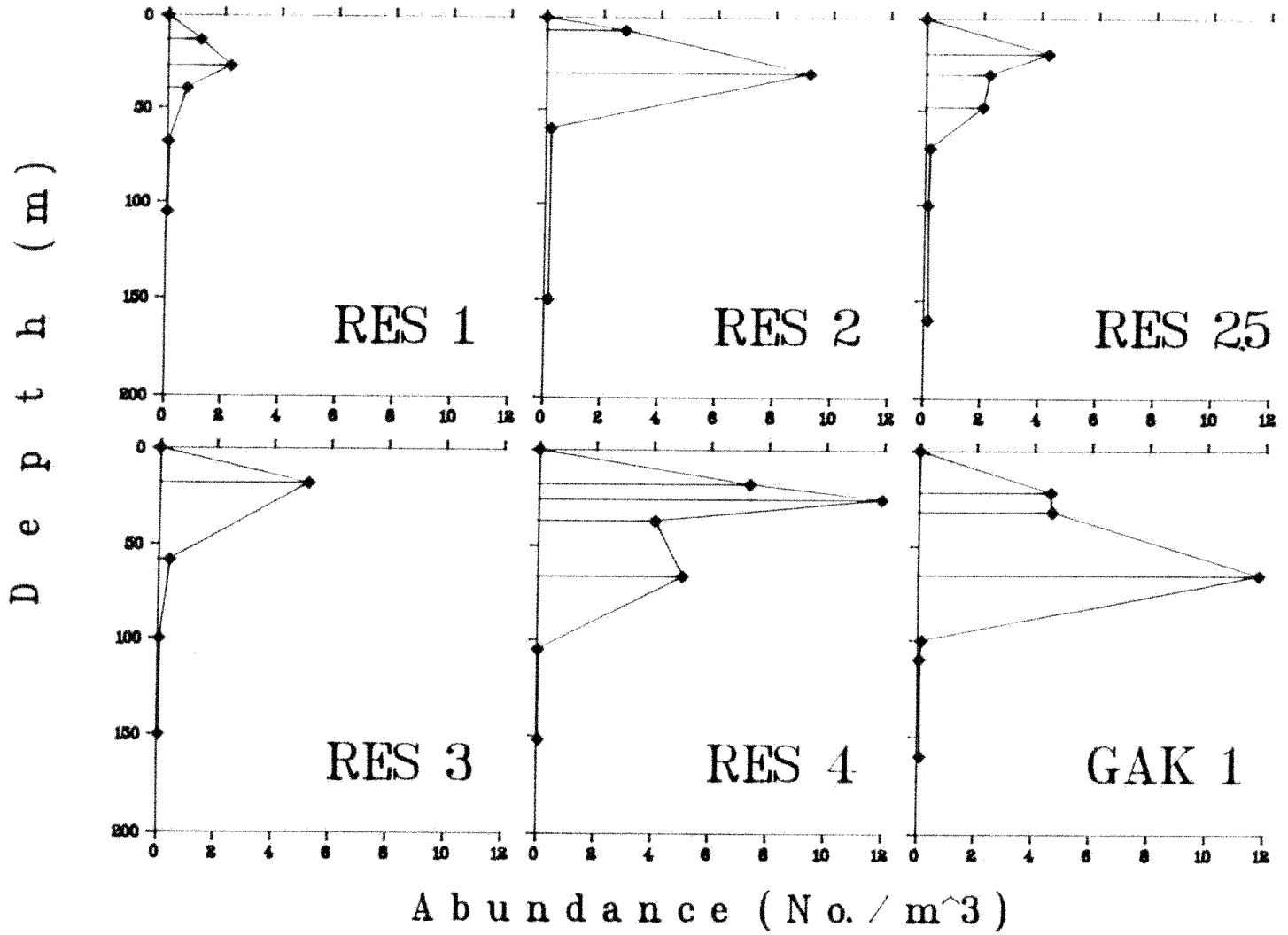


Fig.11 Vertical Distribution of walleye pollock larvae in Resurrection Bay, Alaska, 1-4 May 1989.

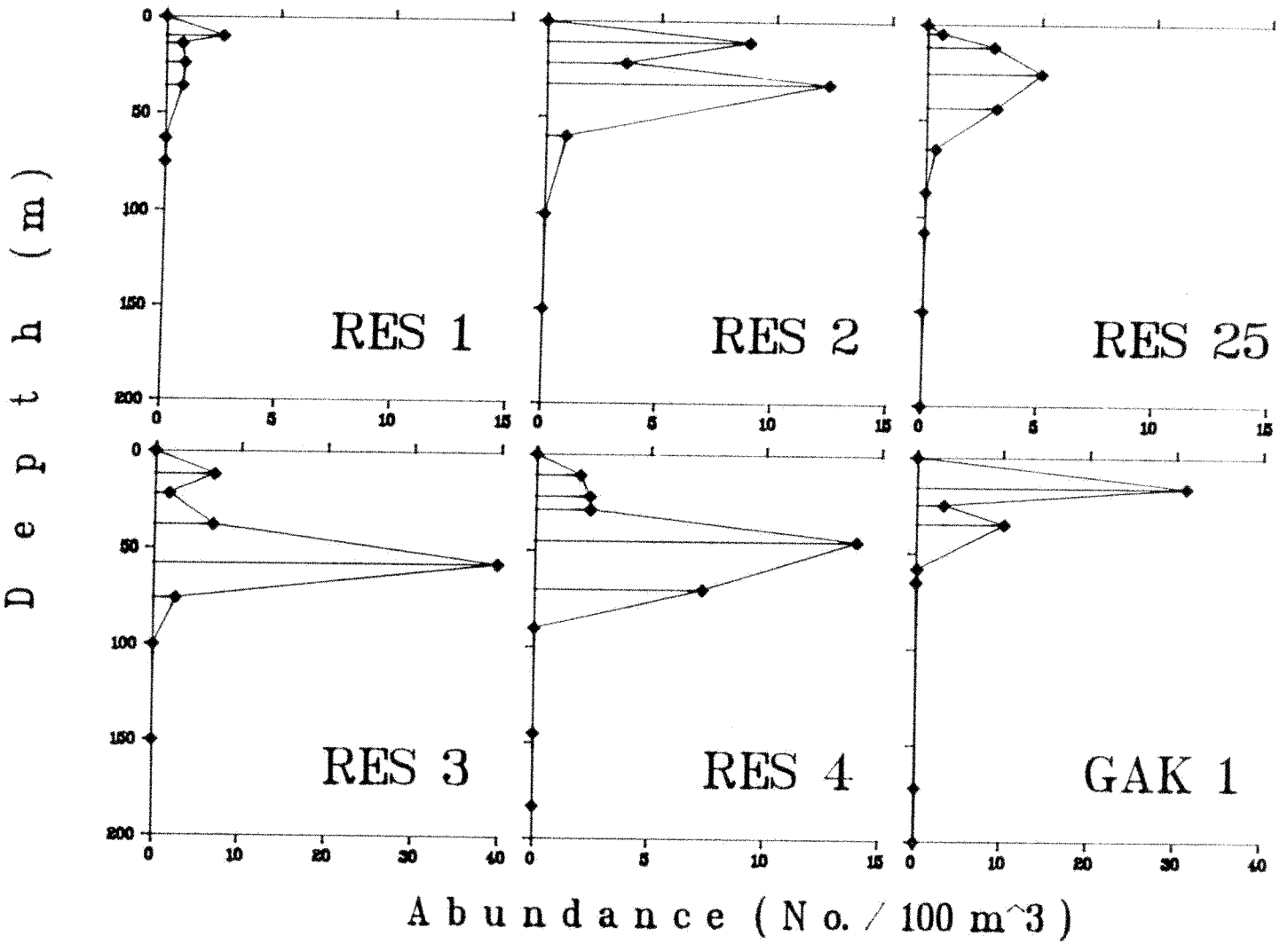


Fig.12 Vertical Distribution of walleye pollock larvae in Resurrection Bay, Alaska, 7-9 June 1989. Note change in scale for RES 3 and GAK 1.

density occurred at depths between 10 m (RES 1) and 58 m (RES 3). The vertical distribution in early June showed no apparent pattern in relation to station location.

Abundance

Using the vertical distribution profiles I estimated larval abundance at each station by integrating over the upper 100 m. In May estimated abundances ranged from 60 larvae m^{-2} at RES 1 to 575 larvae m^{-2} at GAK 1 (Table 4). Abundances at the outer stations were much higher than in the inner basin due to high larval densities below 50 m at RES 4 and GAK 1.

In June abundances ranged from 0.45 larvae m^{-2} at RES 1 to 10.28 larvae m^{-2} at RES 3. The estimated abundances were again higher at the outer stations. The highest abundance was found above the sill, as the largest number of larvae was captured at RES 3 at 58 m. Abundance averaged across all stations decreased from 281 larvae m^{-2} in early May 1989 to 4.59 larvae m^{-2} five weeks later.

It should be noted that a net with the same mesh size was used during both cruises. Larvae caught in June were much larger and greater escapement was expected, resulting in more conservative estimates of larval density and abundance for June.

Larval size distribution

Larval size and depth

Mean SL of larvae preserved in isopropyl alcohol differed with depth at all stations (Table 5). Both a Student t-test and a Mann-Whitney test of differences between means showed highly significant differences between the shallow and deep samples at RES 1, 2, 2.5, 3 and RES 4 (Table 6). An ANOVA for station GAK 1 suggested highly significant differences as well ($F=42.331$; $p<0.001$). Multiple

Table 4: Abundances of larval walleye pollock in Resurrection Bay in early May and early June 1989

Station	Abundances (larvae m^{-2}) early May	early June
RES 1	60	.5
RES 2	285	4.0
RES 2.5	137	1.8
RES 3	168	10.3
RES 4	461	5.2
GAK 1	575	5.8

Table 5: Range, mean SL, variance, and mean SL corrected for date of sampling for larvae collected 1-4 May 1989 and preserved in isopropyl alcohol.

station	depth (m)	number of larvae	range (mm)	mean SL (mm)	variance	corrected mean SL
RES 1	13	188	4.81 - 10.20	7.75	1.15	7.39
	39	91	4.49 - 9.31	6.81	.853	6.45
RES 2	7	481	4.07 - 15.03	7.61	2.01	7.25
	60	24	4.59 - 8.40	6.67	1.02	6.31
RES 2.5	19	678	2.65 - 9.69	5.76	1.17	5.58
	90-110	36	5.22 - 8.93	6.50	.625	6.32
RES 3	18	919	3.37 - 10.68	6.27	1.18	6.09
	58	95	4.15 - 9.58	6.91	.881	6.73
	100	13	5.06 - 8.79	6.68	1.24	6.50
RES 4	18	730	3.78 - 9.15	5.85	.857	5.85
	66	735	3.58 - 8.31	6.09	.498	6.09
GAK 1	22	983	2.87 - 8.81	5.37	.779	5.55
	32	299	3.62 - 7.88	5.45	.707	5.63
	65	2534	3.80 - 8.61	5.90	.396	6.08
	100	29	4.31 - 6.84	5.65	.368	5.83

Table 6: Comparison of mean SL by depth for larvae preserved in isopropyl alcohol. For depths of samples, mean SL and variance see Table 5. Results from T-test and Mann-Whitney test for two sample comparisons. Results from ANOVA for multiple comparisons.

Comparison (A vs.B in m)	Student-t	p	Mann-Whitney U-statistic	p	Conclusion
RES 1: 13 vs. 39	7.116	< .001	12586	< .001	A ≠ B
RES 2: 7 vs. 60	3.202	.001	7255	.001	A ≠ B
RES 2.5:19 vs.100	4.082	< .001	6272	< .001	A ≠ B
RES 3: 18 vs. 57	5.556	< .001	27223	< .001	A ≠ B
RES 4: 18 vs. 65	5.301	< .001	178660	< .001	A ≠ B

GAK 1: 22, 32, 65 and 100m ANOVA: F = 42.331 P < .001

Tukey-HSD multiple comparison

Comparison (A vs.B)	pairwise comparison probabilities	Conclusion (α=0.05)
22 vs. 32	.010	reject H_o: A = B
22 vs. 32	.103	accept H_o: A = B
22 vs.100	1.000	accept H_o: A = B
32 vs. 65	1.000	accept H_o: A = B
32 vs.100	1.000	accept H_o: A = B
65 vs.100	1.000	accept H_o: A = B

comparison tests were employed to locate the differences. Results from a Tukey HSD test showed significant differences in mean standard length between samples from 22 m and 65 m at GAK 1 ($p=0.01$). Differences between any of the remaining pairs were not significant (Table 6).

While significant differences in size with depth existed at all stations, the sign of the differences varied between stations. At the two innermost stations (RES 1 and RES 2) larval size decreased with depth, whereas at all other stations the opposite trend was found, i.e. increasing size with depth, excluding the samples from 100 m at RES 3 and GAK 1. These samples showed a slight decrease in mean SL compared to shallower samples (Table 5).

For larvae preserved in ethyl alcohol, between depth comparisons could only be made for stations RES 2.5 and RES 4 because multiple depth samples were not available from the other stations (Table 7). Larval size seemed to generally increase with depth at RES 2.5 and to decrease with depth at RES 4. Table 8 shows test statistics for an ANOVA and pairwise comparison probabilities resulting from a Tukey HSD test. While the ANOVA led to rejection of the Null-hypothesis that mean SL is the same at each depth, a Tukey HSD test did not detect any significant differences between pairs at $\alpha = 0.05$.

Larval Size and Location

To compare larval size between stations mean SL was corrected for sample dates, using growth rates. Tables 5 and 7 show mean SL, variance and corrected mean SL for all samples collected in the upper 100 m. Samples below 100 m were not included in the following analyses, since the numbers of larvae were small.

Comparisons were again made separately for larvae preserved in

Table 7: Range, mean SL, variance, and mean SL corrected for date of sampling for larvae collected 1-4 May 1989 and preserved in ethyl alcohol.

station	depth (m)	number of larvae	range (mm)	mean SL (mm)	variance	corrected mean SL
RES 1	25-28	303	3.64 - 10.80	6.89	1.08	6.51
RES 2	30	1327	4.20 - 10.22	6.36	.964	5.98
RES 2.5	19	425	4.09 - 10.61	6.58	1.578	6.39
	30	546	4.31 - 9.64	6.46	.986	6.27
	48	490	4.61 - 8.96	6.63	.559	6.44
	70	45	4.61 - 9.28	6.71	1.62	6.52
	250-0	448	4.03 - 9.87	6.60	.908	6.41
RES 4	18	773	4.01 - 10.30	6.87	1.34	6.87
	26	1490	4.25 - 13.40	6.73	1.50	6.73
	37	437	3.74 - 10.28	6.09	1.16	6.09

Table 8: Comparison of mean SL by depth for larvae preserved in ehtyl alcohol. For mean SL and variances see Table 5. Results of ANOVA.

RES 2.5: 19, 30, 48, 70m ANOVA: $F = 9.341$ $P < .001$

Tukey - HSD test

comparison (A vs.B)	pairwise comparison probability	conclusion (α=0.05)
19 vs. 48	.327	accept H_o: A = B
19 vs. 30	.767	accept H_o: A = B
19 vs. 70	.864	accept H_o: A = B
30 vs. 48	.987	accept H_o: A = B
30 vs. 70	1.000	accept H_o: A = B
48 vs. 70	1.000	accept H_o: A = B

RES 4: 18, 26, 37m ANOVA: $F = 9.341$ $P < .001$

Tukey - HSD test

comparison (A vs.B)	pairwise comparison probability	conclusion (α=0.05)
18 vs.37	.105	accept H_o: A = B
26 vs.37	.146	accept H_o: A = B
18 vs.26	.994	accept H_o: A = B

isopropyl alcohol and ethyl alcohol. For larvae preserved in isopropyl alcohol, the depth of the shallowest samples included in this analysis ranged from 7 m at RES 2 to 22 m at GAK 1. Since we sampled over a 4-day period, the measured lengths will differ due to growth during this period. Thus, standard length was corrected for date of sampling using a growth rate of 0.18 mm/day, which I obtained for walleye pollock larvae preserved in isopropyl alcohol (see below). May 2 was arbitrarily chosen as "day 0". Lengths of larvae sampled before this date were increased by 0.18 mm/day to account for growth. Similarly 0.18 mm was subtracted from mean SL for each day larvae were sampled after May 2. The corrected mean SL will be referred to as mean SL in the following discussion.

Both a parametric ANOVA and a non-parametric ANOVA by ranks (Kruskal-Wallis test) showed that mean SL differed significantly between stations ($F=390.9$, $p<0.001$; Kruskal-Wallis test statistic=746.5, $p<0.001$). A Tukey HSD multiple comparison test indicated significant differences between the innermost station pair (RES 1 and RES 2) and each of the stations outside RES 2 (RES 2.5, 3, 4, GAK 1, see Table 9). Among the outside stations the only significant difference was found between RES 3 and GAK 1 (Table 9). A Tukey type nonparametric multiple comparison (Zar 1984), using ranked data, yielded identical results except for one case. An additional significant difference was found between mean SL at RES 3 and RES 2.5 ($q=6.625$, $p<0.001$).

When samples from each station were pooled and mean SL compared between stations, results were very similar. An ANOVA showed a highly significant difference in mean SL ($F=80.00$, $p<0.001$). A Tukey HSD multiple comparison indicated again significant differences ($\alpha=0.05$) between both of the two innermost stations and each of the

Table 9: Comparison of mean SL by station for larvae preserved in isopropyl alcohol. Most shallow sample from each station only. For mean SL and variances see Table 5.

ANOVA results: $F = 390.923$ $p < .001$

Tukey - HSD test, pairwise comparison probabilities:

Station (depth)	RES 1 (13m)	RES 2 (7m)	RES 2.5 (19m)	RES 3 (18m)	RES 4 (18m)	GAK 1 (22m)
RES 1	1.000					
RES 2	1.000	1.000				
RES 2.5	.001	.000	1.000			
RES 3	.003	.003	.057	1.000		
RES 4	.002	.002	1.000	.126	1.000	
GAK 1	.001	.001	.195	.003	.066	1.000

stations outside RES 2.

The results indicated that the stations can be grouped by location, stations RES 1 and RES 2 in one group, and stations RES 2.5, 3, 4, and GAK 1 in another group. Mean SL for a station from one group differed significantly from the mean SL for any station from the other group, while there was only one significant difference at the $\alpha=0.05$ level within these groups (Tukey test, Table 9).

The size differences translate into an age difference of 8.5 days between the average at the inner stations (RES 1 and RES 2) and that at the outer stations (RES 2.5, 3, 4 and GAK 1). The age was calculated using equations derived from growth analysis (see below). The average age of larvae collected at stations RES 1 and RES 2 was estimated at 15.1 days. That at the other four stations was estimated to be 6.6 days. Age was calculated relative to May 2.

Larvae preserved in ethyl alcohol were available from only four stations (Table 7). Differences in mean SL between these stations were compared between the shallowest samples only, since at RES 1 and RES 2 larvae from only one depth were preserved in ethyl alcohol. Lengths were corrected as described earlier for date of sampling using a growth rate of 0.19 mm/day, obtained for a sample preserved in ethyl alcohol (RES 4, 18 m, see below). The shallow samples used in this analysis were collected between 18 m and 30 m. Both a one-way ANOVA and a non-parametric test resulted in rejection of the Null hypothesis that the samples came from the same population ($F=28.59$, $p<0.001$; Kruskal-Wallis test statistic=80.68, $p<0.001$). However, a Tukey HSD test failed to show a significant differences in SL for any of the pairwise comparisons (Table 10). Comparisons of age would yield identical results since they were derived from mean SL by linear transformations.

Table 10: Comparison of mean SL by station for larvae preserved in ethyl alcohol. Most shallow sample from each station only. For mean SL and variances see Table 7.

ANOVA results: $F = 28.586$ $p < .001$

Tukey - HSD test, pairwise comparison probabilities:

Station (depth)	RES 1 (26m)	RES 2 (30m)	RES 2.5 (30m)	RES 4 (18m)
RES 1	1.000			
RES 2	.196	1.000		
RES 2.5	.490	1.000	1.000	
RES 4	1.000	.112	.579	1.000

Results from these tests differed depending on the preservatives that were used. While results for larvae preserved in ethyl alcohol were inconclusive, the results for larvae preserved in isopropyl alcohol suggest that the stations can be divided into two distinct groups on the basis of larval size. Larval size at stations RES 1 and RES 2 seemed to be significantly larger than at all stations outside RES 2.

Growth rates

Growth rates were determined for larvae collected 1-4 May 1989 at station RES 2 in the inner basin and station RES 4 in the outer basin using estimated ages obtained by the otolith increment technique. Readability of the pollock otoliths was in general rather poor compared to otoliths from other species. A distinct dark band around the nucleus was visible in most cases and was counted as increment one. Daily increments after day one were generally much fainter with the exception of a few dark bands that were present in other areas of the otolith. Usually a dark band could be distinguished in the vicinity of increment 5, presumably corresponding to first feeding (K. Bailey, NMFS, Seattle, pers. comm.). Frequently another distinct increment occurred around days 14-16. Occasionally much fainter rings could be distinguished between consecutive increments. They were assumed to be subdaily increments (K. Bailey pers. comm.).

At station RES 2, 62 larvae collected at 7 m on May 4, 1989 were measured and dissected to remove otoliths, of which 54 could be aged. The increment count ranged from 6 to 40 increments for larvae between 5.1 mm and 11.1 mm SL. A linear regression model relating mean SL and increment count yielded a growth rate of 0.18 mm/day

(r^2=0.75, Fig. 13). The 95% confidence interval for this growth rate was 0.18 $\pm$ 0.028 mm/day. From a sample collected at RES 4, 18 m on May 2, 1989, 38 larvae between 5 and 25 days were aged, ranging in length from 5.3 mm to 10.1 mm. The growth rate at this station was estimated to be 0.19 $\pm$ 0.016 mm/day (r^2=0.79, Fig. 13).

In addition to length at age, I examined the relationships between otolith size and age and between standard length and otolith diameter. The regressions of otolith diameter on increment count resulted in a much tighter fit for both stations (r^2=0.85 and r^2=0.91 for RES 2 and RES 4; Fig. 14). Regressions of length on otolith size indicated a close relationship between body length and otolith diameter for the limited size range studied here (r^2=0.83 and r^2=0.86; Fig. 15).

I compared the regression lines of standard length on increment count from RES 2 and RES 4 using the t-statistic according to Zar (1984) and found no significant difference between the slopes ($t=1.048$; $0.20<p<0.50$). Thus the null hypothesis that both stations show the same growth rate (equal slopes) is not rejected. A common slope for both data sets was computed using a weighted regression coefficient (Zar 1984). The resulting combined growth rate for all walleye pollock larvae in Resurrection Bay was 0.18 mm/day.

A comparison of elevations (y-intercept) of the two regression lines (Zar 1984) also resulted in no significant difference ($t=1.797$; $0.05<p<0.10$). Since the two subsamples used for aging came from different preservatives, no common regression equation was computed. Separate regression equations from RES 2 and RES 4 were used to calculate ages for larvae in isopropyl alcohol and ethyl alcohol. The regression equations relating length and age were:

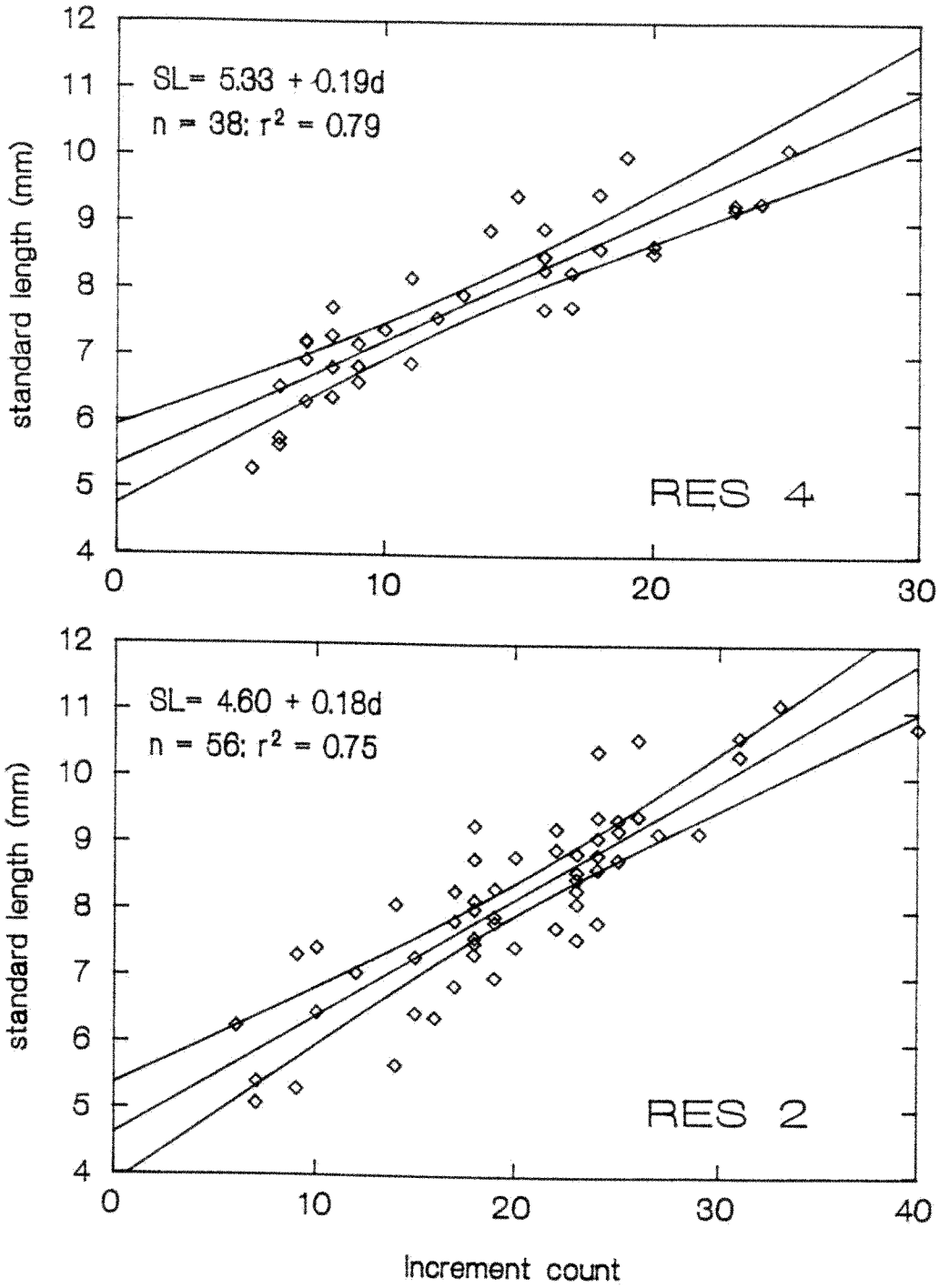


Fig.13 Linear regression of length on increment count for otoliths from walleye pollock at stations RES 2 and RES 4, Resurrection Bay, Alaska, May 1989.

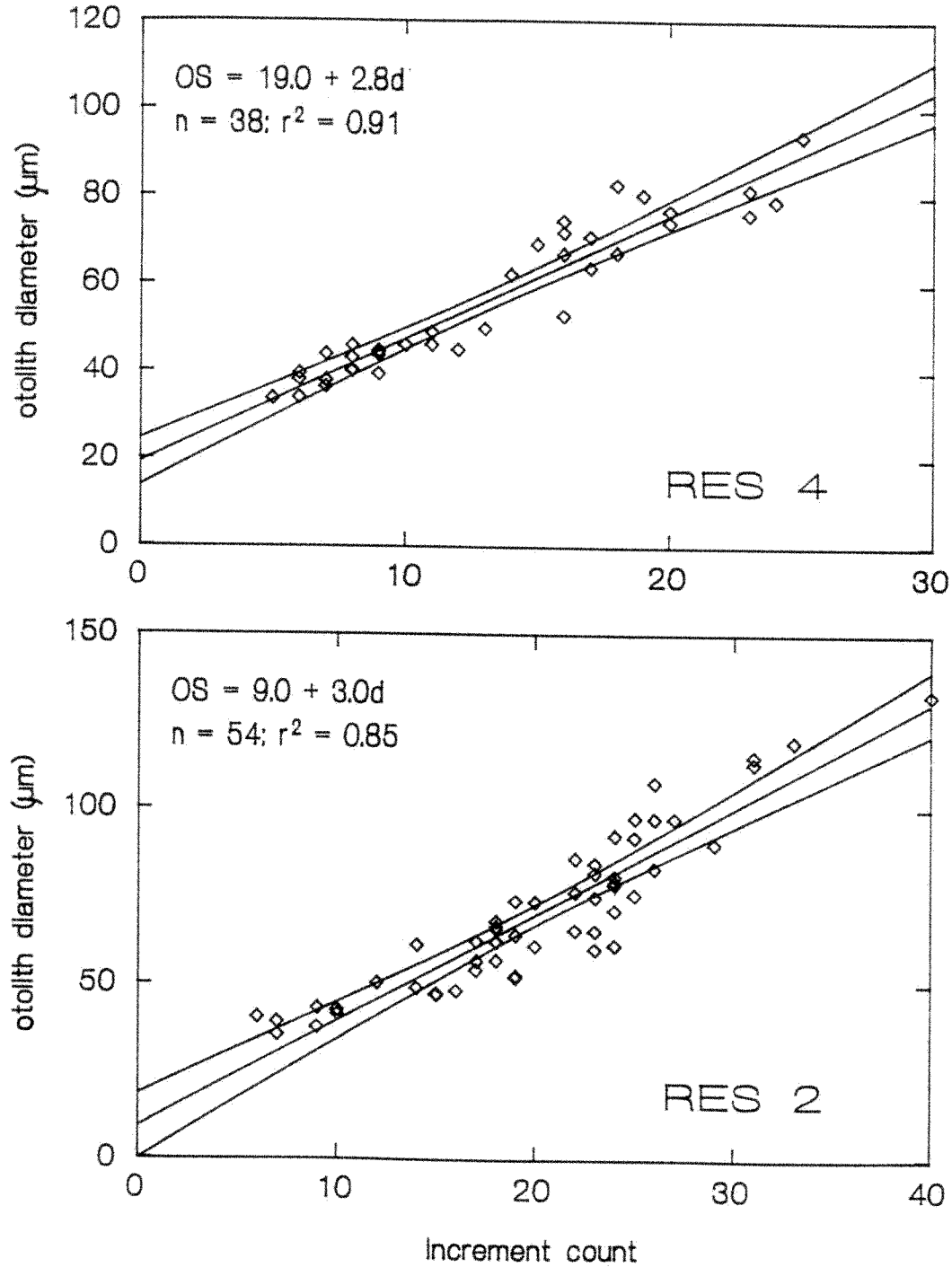


Fig.14 Linear regression of otolith diameter on increment count for otoliths from walleye pollock at stations RES 2 and RES 4, Resurrection Bay, Alaska, May 1989.

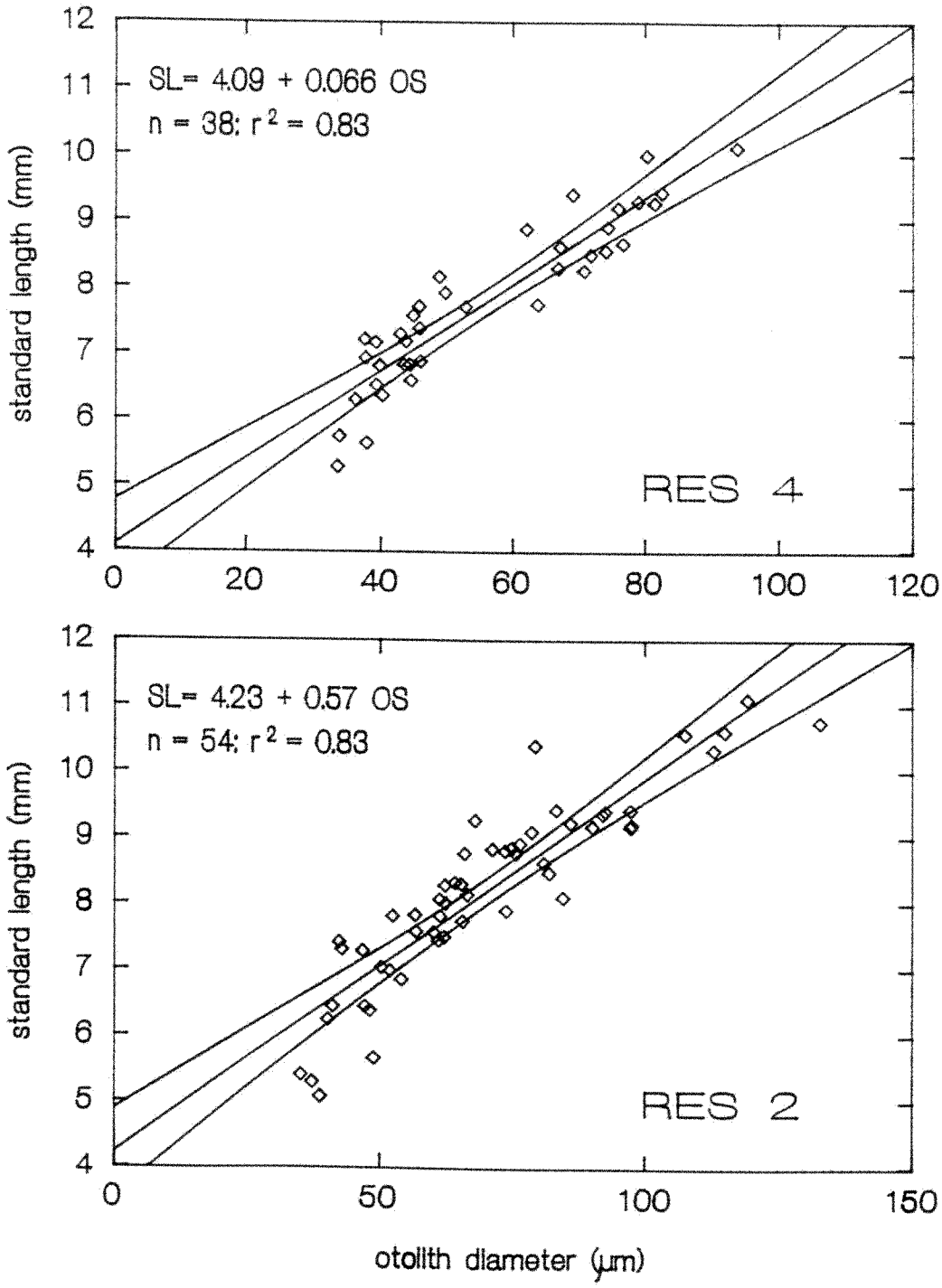


Fig.15 Linear regression of standard length on otolith diameter for otoliths from walleye pollock at stations RES 2 and RES 4, Resurrection Bay, Alaska, May 1989.

RES 2 (ISO): SL = 4.60 mm + 0.18 mm/day * age(days)

RES 4 (EtOH): SL = 5.33 mm + 0.19 mm/day * age(days)

The following equations were used to convert length to ages:

Age = (SL - 4.60)/0.18 for larvae in isopropyl alcohol

Age = (SL - 5.33)/0.19 for larvae in ethyl alcohol

Hatch dates and spawning dates

Hatching dates, as estimated from larval age distribution for all larvae collected 1-4 May, 1989, ranged from April 2 to May 9 with a median on April 25 (Fig. 16). A median spawning date was estimated using hatch date and egg incubation period. Based on the average temperature below 150 m at GAK 1 on April 6, I estimated an average incubation temperature of 5°C. Haynes and Ignell (1983) found an incubation time of 15 days for this temperature. Thus the estimated median spawning date is April 10.

Change in abundance

The abundances of larval pollock changed considerably between the May and June cruises, due to mortality and advection. The daily change in abundance was calculated using differences in larval abundance. Assuming an exponential decrease for the larval pollock population the daily instantaneous rate of change can be calculated as:

$$N_t = N_0 * e^{-zt}$$

where:

N_t = abundance of larvae in June (LO002)

N_0 = abundance of larvae in May (LO001)

z = daily instantaneous rate of change

t = time in days between cruises

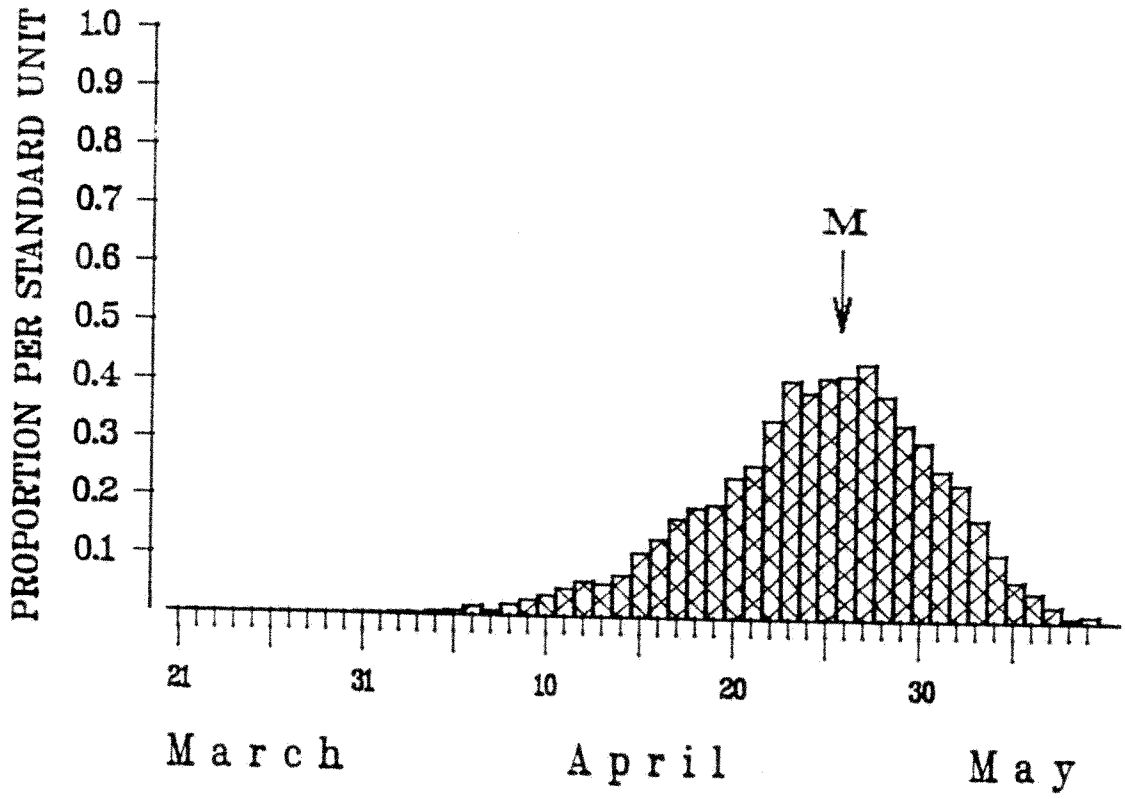


Fig.16 Estimated hatch date distributions of larval walleye pollock collected in Resurrection Bay, Alaska, in early May 1989. M indicates median hatch date.

Based on the total number of larvae caught during the two cruises (N_t = 420, N_0 = 16950) the daily rate of change was calculated as z=0.104. The time between the mid-points of LO001 and LO002 was 35.5 days. This estimate assumes equal sampling designs and equal amounts of effort during both cruises, which was not the case.

A better estimate may be obtained using larval abundances averaged over all 6 stations. The average abundance decreased from 281 larvae m^{-2} in May to 4.59 larvae m^{-2} in June. Using N_t = 4.59 and N_0 = 281 yielded a similar rate of change of 0.115. An even better estimate could be obtained if abundances at each station would be weighted according to the area represented by the station. Because of the highly dynamic environment in Resurrection Bay it is difficult to estimate the area represented by each station and no attempt was made to do so.

DISCUSSION

Hydrography

Resurrection Bay, like other Alaskan fjords, e.g. Endicott Arm, Russell Fjord, and Port Valdez (Nebert 1972, Reeburgh et al. 1976, Colonell 1979), does not show a dominant freshwater-driven surface circulation characteristic of many fjords. The relatively small volume of freshwater discharge at the head of Resurrection Bay and the proximity of the ACC at its mouth suggest that circulation driven by wind, tides, and atmospheric pressure differences might be more important.

The few available current observations indicate that flow at the surface is strongly influenced by short term variations in the free surface elevation at the mouth of the fjord. During periods of intense downwelling and during transitions from upwelling to downwelling the surface flow inside Resurrection Bay is likely to be upfjord. Upwelling events seem to favor downfjord flow at the surface.

Another factor that will strongly influence surface flow is wind, which can reverse the surface outflow of low salinity water. During periods of downwelling, associated with low pressure systems in the Gulf of Alaska, winds are predominantly offshore i.e. downfjord. Downfjord winds will favor surface outflow in the fjord and thus counteract the onshore Ekman transport. The relative importance of wind, tides and density differences for the surface circulation in Resurrection Bay cannot be evaluated at this time.

During flooding and ebbing tides the effects of wind and surface elevation will be masked by tidal flow. However, the observed flow patterns suggest that either upwelling conditions on the

shelf or other factors like wind can override tidal flow and may determine the surface circulation in Resurrection Bay. These factors are characterized by short term oscillations on the order of a few days. The upper layer circulation in Resurrection Bay can thus be characterized by highly variable events on a similar time scale.

The general relaxation of downwelling along the southern coast of Alaska during the summer suggests that surface outflow will be favored during this period. The increased freshwater input also favors surface outflow, while wind direction is primarily onshore in the summer and favors upfjord flow at the surface. Current observations between June and October 1989 show that the average flow during this period was upfjord near the surface (15 m) at a station located just outside the sill. However, the current meter may have been below an offshore moving upper layer. Even if the surface flow at the mooring location was upfjord, net flow across the width of the fjord may not have been up-fjord. The flow may have been divided in the horizontal plane with water entering the fjord along one side of the basin and a returning along the opposite shore. There is evidence from ADCP transects across the fjord for such a flow pattern (T. Weingartner, pers. comm.). The salinity and temperature transects across GAK 1 show low salinities and high temperatures near both shores (Fig. 7, Fig. 8) which is also consistent with the suggested flow pattern. Alternatively, subsurface outflow must compensate for surface inflow.

The upper layer circulation will play an important part in determining larval distribution in the bay, since these were concentrated in the upper 50-70 m. Surface inflows and outflows will advect larvae across the sill in both directions. If the average flow at the surface is upfjord, it may result in a trend toward

accumulation of larvae within the fjord if they maintain their position in the upper layers.

We may have observed the advection of larvae into Resurrection Bay in early May 1989. Evidence for such an event can be found in the observed salinity profiles at RES 2.5 and GAK 1 (Fig. 6) and in the larval size distribution at these stations. The salinity profile at RES 2.5 is anomalous in that it shows no pronounced freshwater lens like the other stations inside the sill. It is very similar to the salinity profile at GAK 1. The high surface salinity at GAK 1 indicates the presence of shelf water at this station, which is much less diluted than water inside the bay or close to shore. However, this cannot explain the high surface salinity at RES 2.5, which is located inside the sill and should receive significant amounts of runoff. The fact that both temperature and salinity in the upper 20 m are almost identical at stations RES 2.5 and GAK 1 and that RES 2.5 was sampled two days after GAK 1 suggests that high salinity surface water from the outer basin may have been advected across the sill into the inner basin. This is in agreement with the observation that larvae sampled at RES 2.5 had a mean standard length very close to that at GAK 1, if growth is taken into account. Corrected mean SL was 5.55 mm at GAK 1 and 5.58 mm at RES 2.5 for larvae preserved in isopropyl alcohol. Stations RES 3 and RES 4 are located between GAK 1 and RES 2.5 but do not show elevated surface salinities. RES 4 was sampled one day prior to RES 2.5 and an intrusion of surface water could have occurred after sampling RES 4. At the highest observed current speeds from current meter observations (28 cm/sec on Oct. 17, 1989, without tides) water can be advected upfjord at a rate of 1 km per hour at 15 m. RES 3 was sampled on the same day as RES 2.5 and should show elevated surface salinities, if high salinity water

was advected across the sill. However, the surface salinity at RES 3 was approximately 2 psu lower than that at RES 2.5 on May 3, 1989.

While upper layer circulation is important for larval transport, deep water flows can cause the advection of eggs across the sill, since eggs are generally assumed to be located below 150 m (Kendall and Kim 1989). Like the upper layer circulation deep water exchanges can operate on short time scales with episodic intrusions of dense shelf water across the sill. The current meter data from 200 m depth just outside RES 3 indicates variability in bottom layer flow on time scales of a few days (T. Weingartner, unpubl. data).

Fig. 17 shows density differences between deep water (200-250 m) at GAK 1 and at RES 2.5 for each month, averaged over the past 20 years for which CTD data were available. Deep water renewal predominantly seems to take place in the early spring and summer. Variations in density follow each other closely throughout the summer when relaxation of downwelling allows dense shelf water to rise to sill level and enter the inner basin. The density on the shelf is slightly higher than that in the inner basin from May until October, making deep water renewal possible at least throughout this time period. During the winter months intense downwelling depresses pycnocline depths and thus reduces the average density on the shelf while the deep water landward of the sill remains at a higher density. The water densities at RES 2.5 and GAK 1 first converge between April and May and the density in the deep inner basin increases until July. This increase can only result from an inflow of denser shelf water. After July the densities at 200-250 m both inside and outside the sill decrease, suggesting that deep water renewal no longer takes place, although the potential for renewal remains since the density is still higher on the shelf.

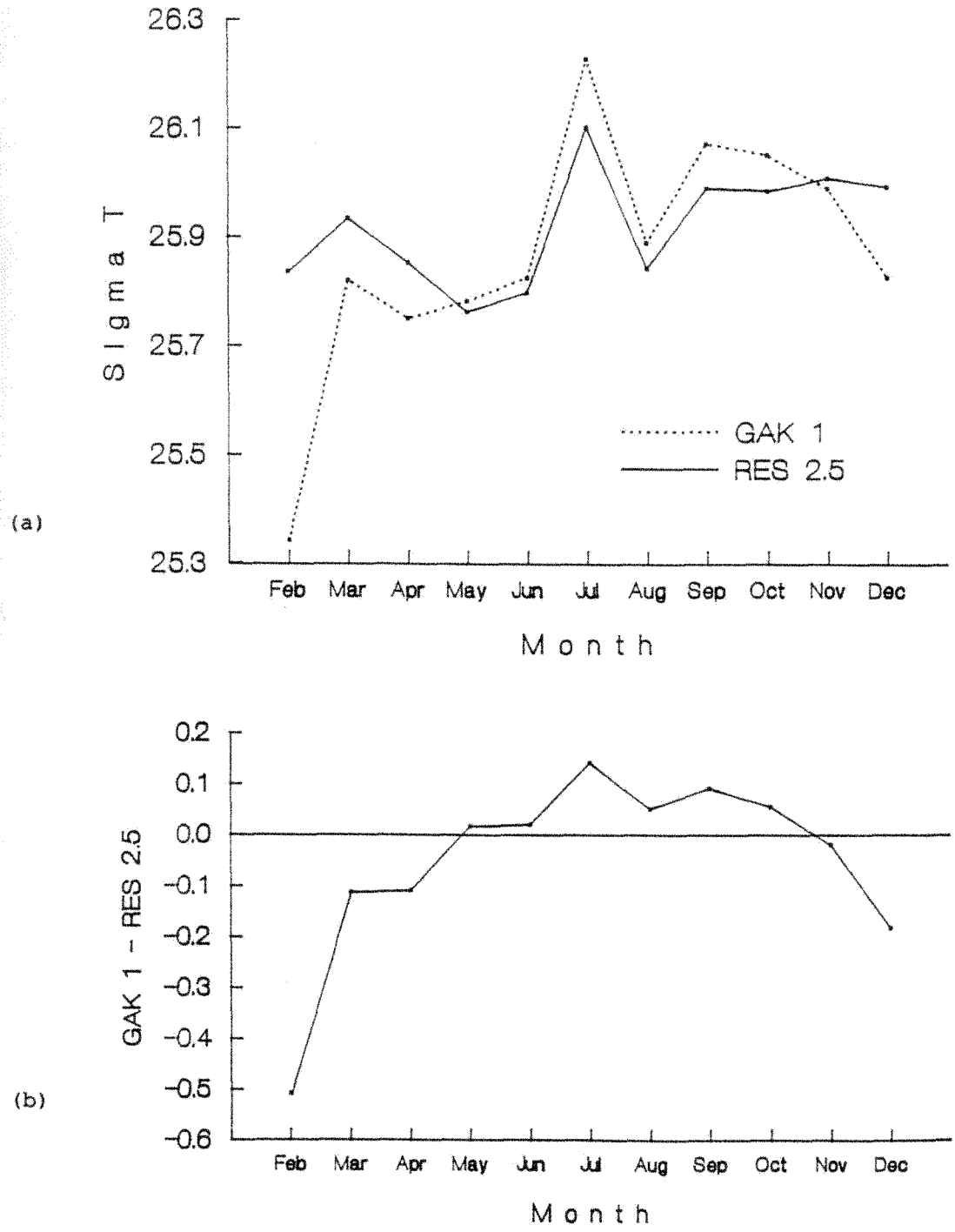


Fig. 17 Sigma T, 200-250 m, at staions RES 2.5 and GAK 1 in Resurrection Bay, Alaska, averaged over the past 20 years, for all months for which data are available (a), and density differences between GAK 1 and RES 2.5 for the same data set (b).

These observations are in agreement with observations by Heggie et al. (1977) that deep water renewal is limited to the period from May to September but contradict Niebauer's (1980) modeling results that deep water renewal is continuous year-round.

If deep water renewal starts in April, the inflowing water masses could transport eggs, which are spawned in early April, into the inner fjord basin, or displace eggs from the inner basin, depending on the location of spawning. The CTD data do not indicate a renewal of deep water between April and May 1989. At RES 2.5 the densities at sill depth and near the bottom remained unchanged, while σ_t at 200 m decreased from 26.05 to 25.90, due to a decrease in salinity (Fig. 18). Temperature at 200 m also decreased slightly over the same time period. This suggests a slow diffusive upward mixing of heat and salt. A deep water renewal on the other hand would have increased the density in the inner basin.

It is equally unlikely that water at an intermediate depth was renewed between April and May. Temperatures at RES 2.5 below about 60 m and above 150 m did not increase during this period and the temperature minimum stayed at 3.3°C (Fig. 5). Water of this temperature could not have entered the fjord from outside, since the temperature minimum at GAK 1 was already above 3.5°C in April and increased to 4°C in May. If neither the deep water nor the intermediate water was exchanged it seems improbable that eggs residing below 150 m could have been advected across the sill into the fjord between April and May of 1989.

Distribution in relation to hydrography

The vertical distribution of larval walleye pollock is influenced by behavioral responses to gravity, light, thermal stratifica-

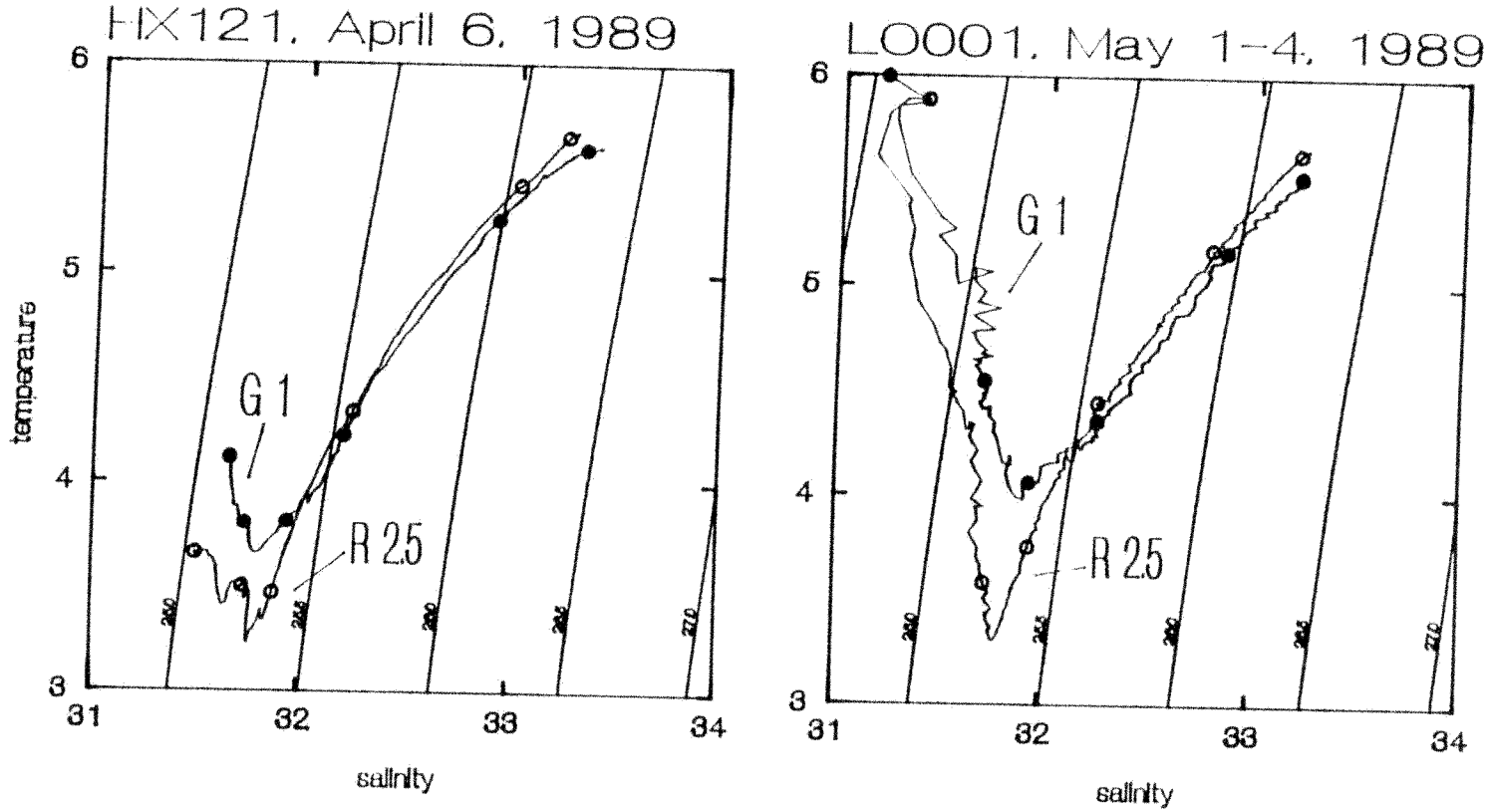


Fig. 18 T-S diagrams for stations RES 2.5 and GAK 1, Resurrection Bay, Alaska, early April and early May 1989. Circles indicate 0, 50, 100, 150, 200, and 250 m.

tion, turbidity and turbulence (Olla and Davis 1990). Even yolk-sac larvae are capable of oriented vertical movement. Olla and Davis (1990) found that larvae moved away from 3°C water in a vertical temperature gradient. Thus, temperature gradients will be reflected in the vertical distribution of walleye pollock larvae.

The results of this study show that the vertical distribution differed between the inner and the outer basin of Resurrection Bay in May 1989. Larvae at the outer stations, RES 4 and GAK 1, were distributed deeper in the water column (Fig. 11). This is consistent with the fact that water temperatures below 40 m were about 1°C warmer at GAK 1 than at all stations inside the sill. Temperatures at RES 4, located between GAK 1 and the sill, were intermediate. Cold water of less than 4°C below 40 m in the inner basin might prevent larvae from descending in the water column, resulting in the observed shallow distribution.

The horizontal distribution of larvae is largely determined by surface layer flow. Surface inflow of water into Resurrection Bay has been observed occasionally and the average flow at the mooring location was upfjord at 15 m between June and October 1989. If this also happens during April and May it provides a mechanism for advection of larvae into Resurrection Bay. Inflow of water at 15 m requires a compensating outflow. If the upper layer flow is divided in the horizontal plane with inflow on one side of the fjord and outflow on the other side larvae may simply be transported through the fjord and their residence time could be very short. Alternatively, if surface inflow is compensated for by subsurface outflow or outflow in a shallow low salinity surface layer, larvae could accumulate inside the fjord if they maintain their vertical position in the water column.

The available evidence suggests that the former mechanism dominates in the outer fjord basin. The relatively high surface salinity at GAK 1 suggests that the water in the outer basin originates on the shelf. A salinity transect across GAK 1 (Fig. 8) shows relatively low salinities at both sides of the transect and higher salinities in the center. This is consistent with an inflow of water along the east side of the outer fjord basin and an outflow along the western shore. The inflow of nearshore water into Resurrection Bay can be seen in satellite images of the area (T. Royer, pers. comm.) and there is evidence from ADCP transects for a counterclockwise circulation in the outer basin (T.Weingartner, pers. comm.). Larvae that originate on the shelf may thus be carried counterclockwise through the outer basin. Larvae could be carried into the inner fjord by intrusions of surface water across the sill. We might have observed such an intrusion between May 1 and May 3 1989 as discussed above.

The length-frequency distribution for larvae at RES 1 and RES 2 indicates that larvae accumulate there. Fig. 19 shows a multimodal length distribution and a wide range of measured lengths for both RES 1 and RES 2, whereas all the other stations show a more narrow, unimodal distribution. This distribution could be the result of several intrusions of surface water and larvae into the inner fjord. The suggested mechanism for advection of larvae into Resurrection Bay is illustrated in Fig. 20. However, accumulation of larvae at the inner stations is not supported by the abundance estimates for these stations. During both the May and June cruises numbers of larvae were higher at the outside stations. Part of this difference could be due to the larger mortality experienced by larvae at RES 1 and RES 2, since they are significantly older.

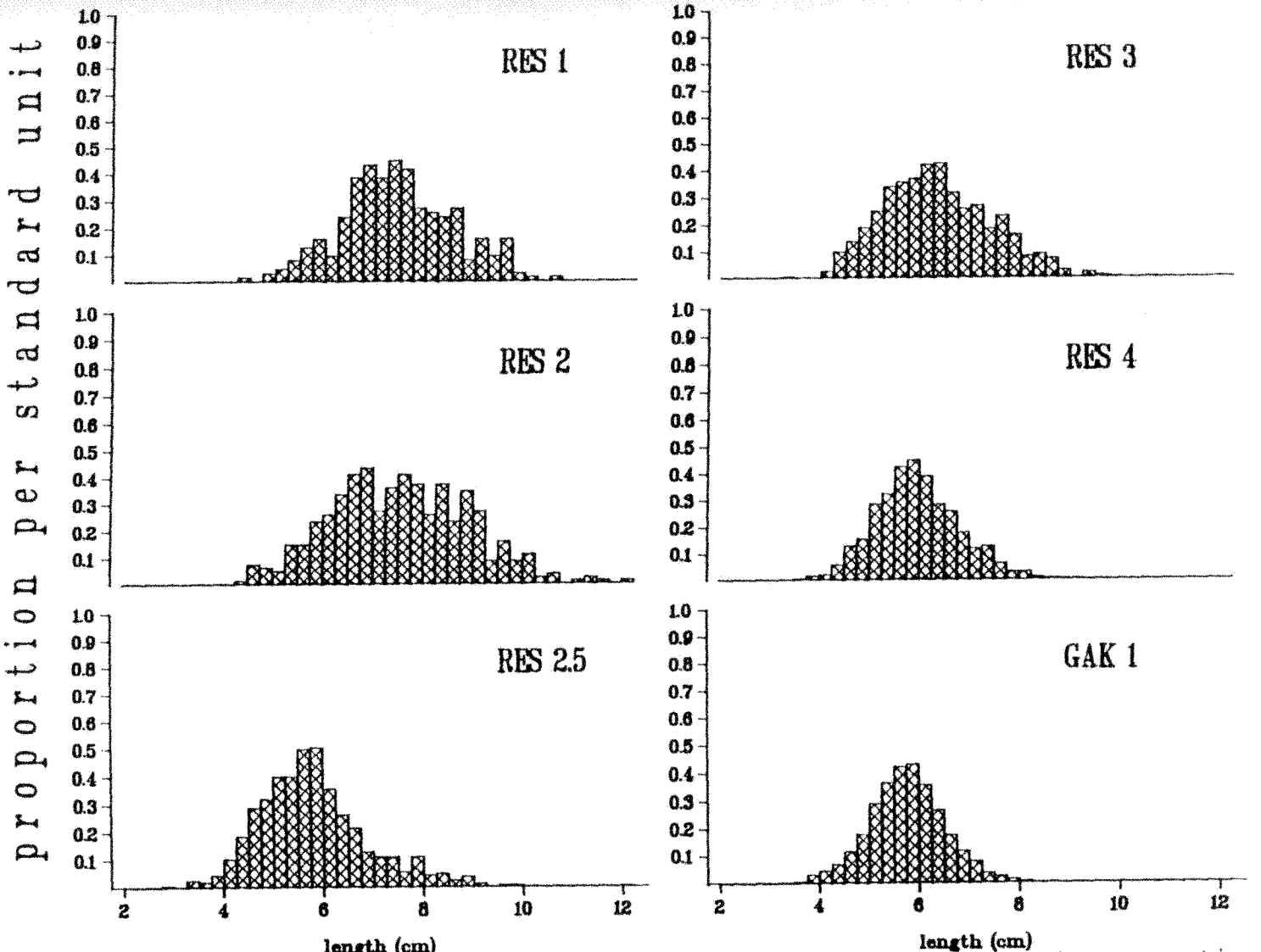


Fig. 19 Length-frequency distributions of larval walleye pollock at six stations in Resurrection Bay, Alaska, 1-4 May 1989.

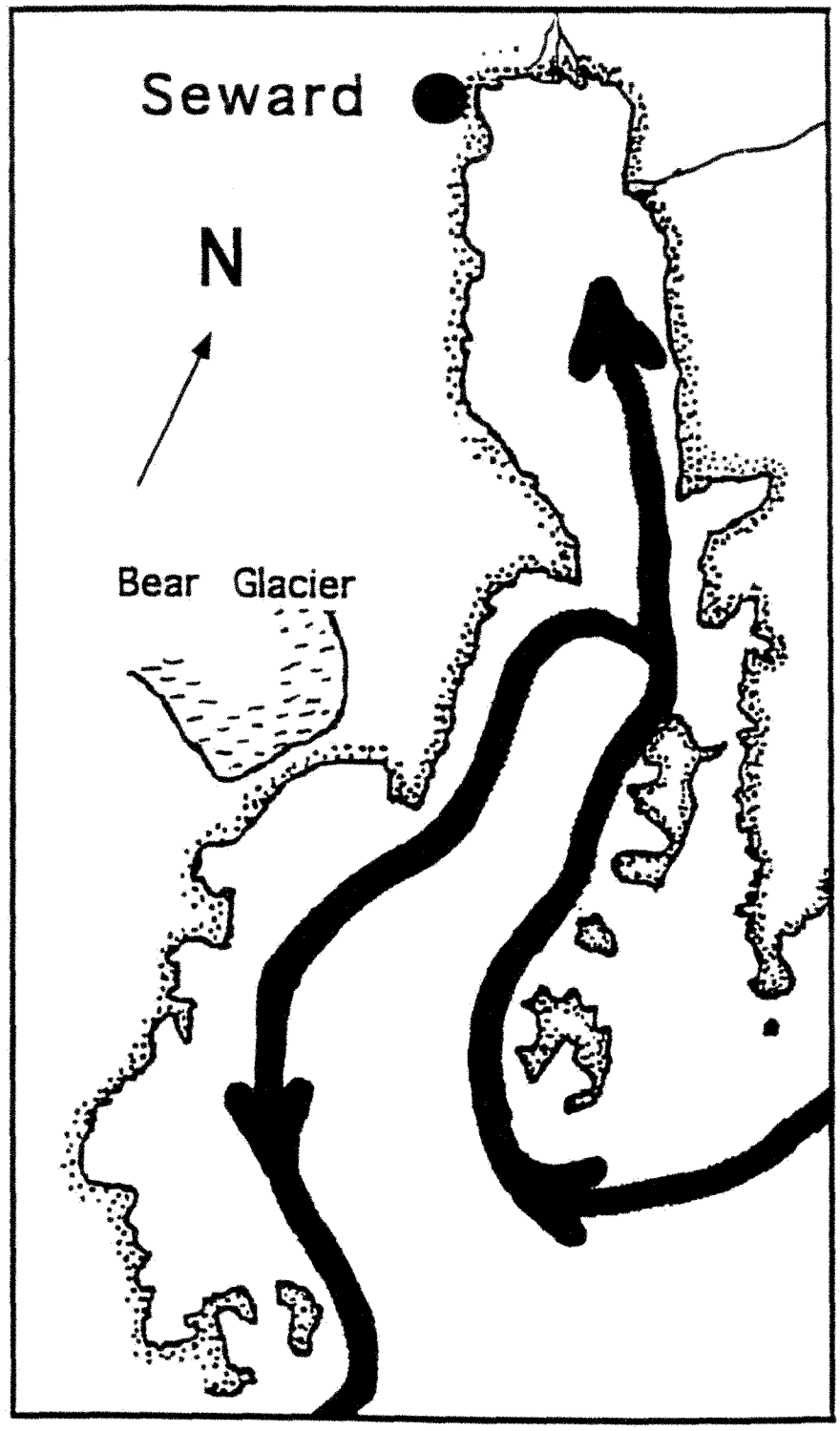


Fig. 20 Hypothesized advection of larval walleye pollock into Resurrectionm Bay, Alaska.

It has been demonstrated for several fjords in Norway that water exchange processes can have a profound influence on the community structure within fjords (Lindahl and Perissinotto 1987). Advective processes can even be the major factor regulating zooplankton biomass in a fjord (Lindahl and Hernroth 1988). Advection of plankton into Resurrection Bay from the shelf is evidenced by the fact that oceanic copepods common in the ACC (*Calanus* spp.) are found in high concentrations inside the fjord in addition to resident species like *Pseudocalanus* (Smith et al. 1991). Larval walleye pollock found inside Resurrection Bay could similarly originate on the shelf and enter the fjord as a result of advective processes.

If advection carries larvae into Resurrection Bay the question arises whether larvae collected in our samples were spawned inside the fjord or originated on the shelf upstream from Resurrection Bay. If spawning had taken place inside the fjord we would have expected to find eggs in the deep samples, since the hatch date distribution indicates that hatching was still in progress. However, none of the samples collected in early May 1989 contained large numbers of eggs. Hydroacoustic surveys indicated the presence of adult walleye pollock in Resurrection Bay during the spawning season in 1983 (A.J. Paul pers. comm.). Regardless of the origin of larvae it is obvious that the larval population in Resurrection Bay is not isolated but is in open communication with the shelf outside the bay and probably with other embayments along the coast.

A direct connection between the mouth of Resurrection Bay and Prince William Sound (PWS), located about 80 km to the east, is indicated in ADCP transects along the Cape Fairfield line (Fig. 3, Johnson et al. 1988). Water exiting PWS through Montague Strait continues to flow southwest along the coast. It exists as a separate

water mass that can be distinguished from ACC water deflected around Montague Island (Luick 1988). These two water masses can often be detected as two separate westward jets across the Cape Fairfield line (Johnson et al. 1988 and Fig. 21). The inshore jet most likely originates in PWS and flows westward towards the mouth of Resurrection Bay. This provides a mechanism by which larvae can be advected from PWS into other bays along the coast. In 1989 high concentrations of walleye pollock larvae were present inside PWS and in Montague Strait (Norcross, unpubl. data). Larvae from Montague Strait are likely to be transported onto the shelf and westward along the coast, since high current speeds have been observed inside the strait and on the shelf (Johnson et al. 1988).

The ACC can thus effectively link plankton communities between inshore bays along the coast. This linkage became evident after the 1989 oil spill in PWS, when oil was carried into Resurrection Bay and other embayments downstream from PWS. Similarly, larval walleye pollock in the upper layer may be advected along the coast and into the bays, provided the transport includes more than a thin surface layer. Future studies should examine the abundance of larval pollock in the ACC.

Abundance

The results clearly indicate that walleye pollock larvae were very abundant in Resurrection Bay and on the shelf outside Resurrection Bay, as represented by GAK 1. If pollock spawn upstream from Resurrection Bay on the shelf, higher concentrations of larvae are likely to be found closer to the point of origin. Larval concentrations inside the fjord in early May 1989 approached those found in the dense larval patch in Shelikof Strait in some years (Kendall et

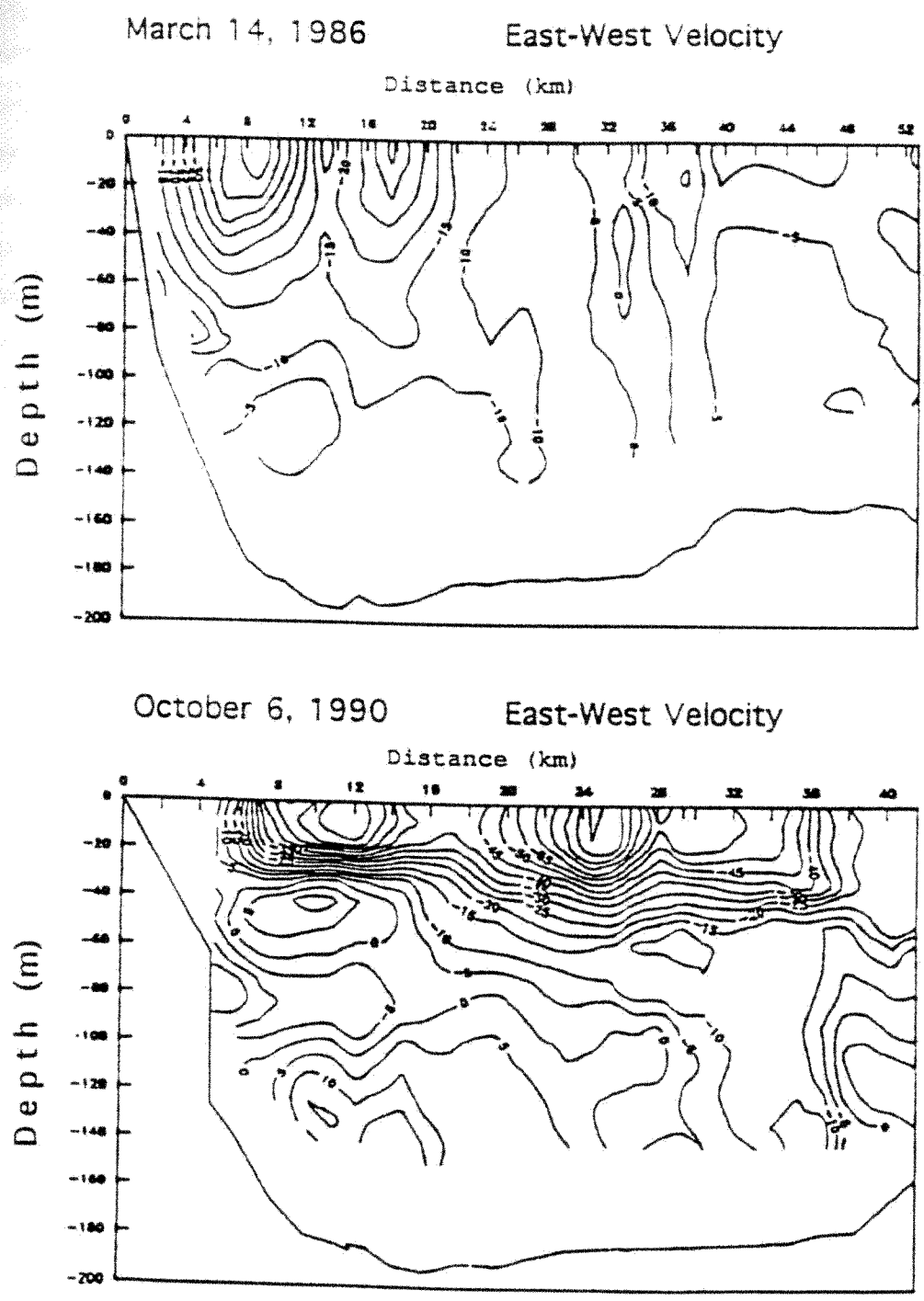


Fig. 21 East-west velocity component (cm/sec; negative values indicate flow to the west) on the Cape Fairfield line in the northern Gulf of Alaska, determined by ADCP.

al. 1987). However, in peak years densities in Shelikof Strait exceed the estimates for Resurrection Bay by one to two orders of magnitude. Abundances of 10,000 larvae m^{-2} were found in the larval patch in Shelikof Strait in 1981 (Bates and Clark 1983). In other years abundances of early larvae range from 0 to 1000 larvae m^{-2} (Kendall et al. 1987) compared to 60 - 575 larvae m^{-2} in this study. Larval concentrations in Funka Bay, Japan decrease from >5000 larvae m^{-2} at some stations in January to 200-400 larvae m^{-2} in early April (Nakatani 1988). They are still relatively high in April, probably because spawning continues throughout March (Kendall and Nakatani 1992). In Auke Bay, Alaska, the observed abundances are much lower with maximum densities of 3 - 15 larvae m^{-2} (Haldorson et al. 1989a). For the Bering Sea no abundance estimates are available, but the total number of larvae caught in bongo tows was very small during surveys in 1978-1979 (Walline 1985).

The abundance estimates in this study have to be interpreted carefully, because we did not consistently sample the same depths at each station and because the estimates were based on few samples for some stations. Average abundance from all 6 stations may not reflect a true average for the entire fjord, since the areas represented by each station differ in size.

Smith et al. (1991) took ichthyoplankton samples in the upper 30 m at RES 1, RES 2.5 and RES 4 every second week from 6 April to 12 July 1988. They found maxima in abundance on 21 April at RES 4, on 5 May at RES 1 and on 18 May at RES 2.5. Maximum densities ranged from 0.8 larvae m^{-3} at RES 1 to 4.13 larvae m^{-3} at RES 4 translating into abundances per unit area of 24 larvae m^{-2} and 123.9 larvae m^{-2}. However, these values are probably underestimates, since they sampled only the upper 30 m, and this study shows high abundances

below 30 m, particularly in the outer fjord basin (Fig. 11).

Additional samples were collected in Resurrection Bay in late April and early May 1991. Qualitative observations suggest that abundances were similar to those estimated for 1989 (Müter, unpublished data). The available data from 1988, 1989, and 1991 suggests that Resurrection Bay is important as a nursery ground for larval walleye pollock. The observed abundances are close to those resulting from the dense spawning aggregations found in Shelikof Strait, Alaska and Funka Bay, Japan (Kendall and Nakatani 1992). Since the extent of the spawning area in the vicinity of Resurrection Bay is unknown, total abundances cannot be compared at present.

Larval size and age distribution

Results indicate that larvae at stations RES 1 and RES 2 were significantly larger and older than larvae at the other stations. This effect was apparent in comparisons of the shallow samples between stations as well as comparisons of the pooled samples between stations for larvae preserved in isopropyl alcohol (Fig. 22). Larvae preserved in ethyl alcohol did not show the same trend. Their mean standard lengths for RES 1 and RES 2 were smaller than the mean standard lengths of larvae in isopropyl alcohol at the same stations. This is contrary to expectations, since shrinkage was observed to be larger in isopropyl alcohol. It is not clear what may have caused these discrepancies.

Since larval length varied significantly with depth, comparisons between samples from different depths have to be interpreted carefully. The shallow samples used for between station comparisons ranged from 7 to 22 m in isopropyl alcohol and from 18 to 30 m in ethyl alcohol. Between depth comparisons showed significant differ-

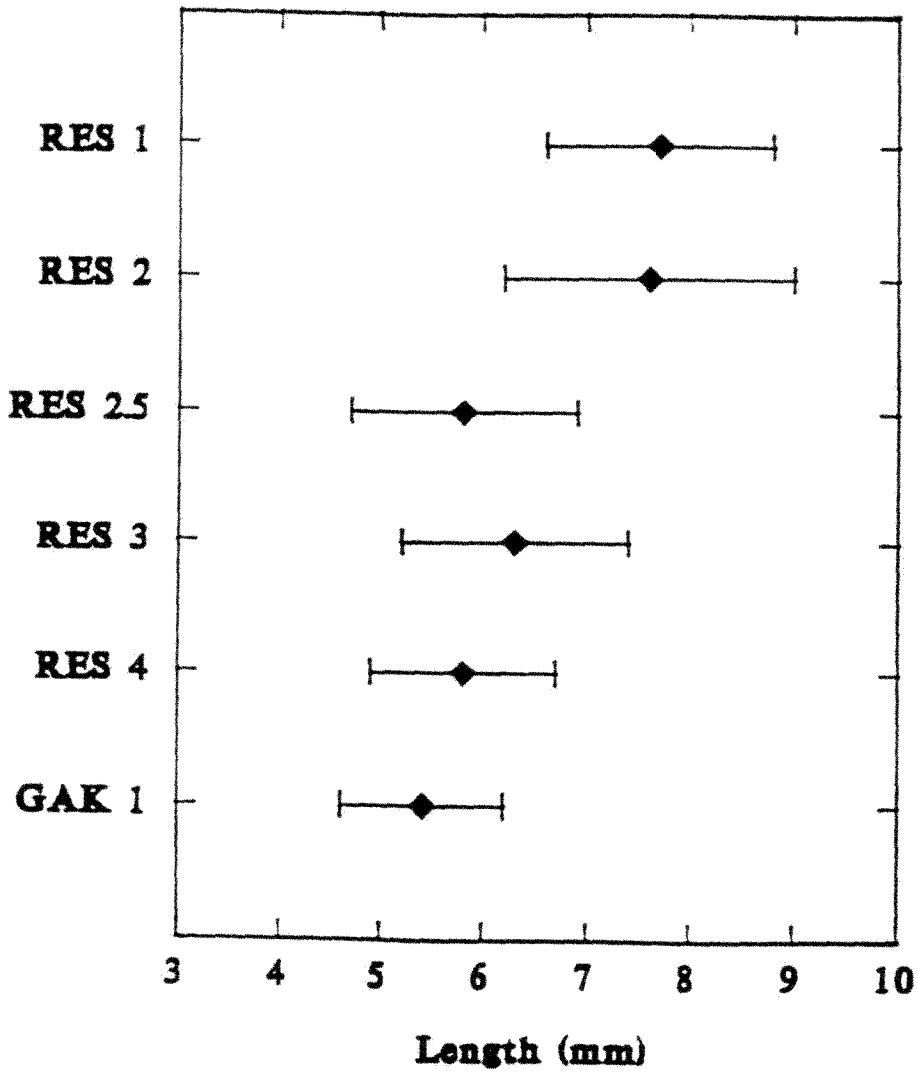


Fig. 22 Mean standard length of walleye pollock larvae from shallow samples taken in Resurrection Bay, Alaska, 1-4 May 1989, and preserved in isopropyl alcohol. Lengths were corrected for date of sampling.

ences between samples that were separated by as little as 26 m (13 m and 39 m at RES 1). Thus significant differences in mean SL may result from differences in the vertical distribution of larvae rather than differences in mean SL between stations.

However, there are other indications that the observed differences reflect true differences in larval age and size between the two innermost stations and the other stations. These can be found in the analyses of the random subsamples that were used in age determination. I compared the means for length, increment count and otolith size between these samples. While no significant difference in mean SL was found between RES 2 and RES 4 ($t=1.529$, $p=0.13$), both increment count and otolith size were significantly greater at RES 2 than at RES 4 ($t=5.334$, $p<0.001$; $t=3.312$, $p=0.001$). Larval length between these samples cannot easily be compared since they were preserved in different preservatives. Because increment count and otolith size will not be affected by preservation, they may be better suited to test for between sample differences in size than the measured SL.

Although measurements of otolith diameter are much more time consuming than length measurements, they are associated with less uncertainties and show less variance. A smaller sample size will be sufficient to estimate the population mean with the same confidence. Inherent uncertainties in length measurements of preserved larvae would thus be eliminated. However, otolith size can only be used as a measure of body size if there is a known relation between the two parameters. Fig. 13 shows that over the limited size range of larvae examined in this study a linear regression could be used to approximate the relation between otolith diameter and body length ($r^2=0.83$ and $r^2=0.86$).

Growth

The growth rates found in this study were close to those reported for larvae from other geographic areas (Table 11). Growth rates for larval walleye pollock in the Gulf of Alaska have been reported from Shelikof Strait and from Auke Bay, which are located at latitudes similar to Resurrection Bay. Shelikof Strait is an estuarine-type system (Kim 1989), which lacks strong stratification, while Resurrection Bay had a well-developed pycnocline in early May 1989. Smith et al. (1991) have suggested that the fjord's strong pycnocline may concentrate nauplii at some depths, improving feeding conditions for larvae. Auke Bay is a relatively shallow bay in Southeast Alaska about 50 m deep. Stratification is established in early May (Pritchett and Haldorson 1989). Walleye pollock larvae in Auke Bay are distributed in the upper 20-25 m, whereas they are deeper in both Shelikof Strait and Resurrection Bay.

Surface temperatures in Resurrection Bay were slightly lower in early May 1989 than those observed in Shelikof Strait and Auke Bay (Kendall et al. 1987, Pritchett and Haldorson 1989). The low temperatures in the inner basin in May reflect delayed warming of the upper water column relative to the shelf. The rise in surface temperature on the shelf might be accelerated due to influx of warmer water with the ACC. Warming will also be delayed inside the fjord due to the presence of steep surrounding mountains which reduce the incoming solar radiation. It may seem that the fjord in early spring provides less favorable growth conditions than the shelf, considering the lower temperatures inside the fjord. However, salinities also differ between the shelf and the fjord, resulting in a more pronounced stratification inside Resurrection Bay (Fig. 6). Stratification of the water column will reduce vertical mixing and

Table 11: Growth of larval walleye pollock in the Gulf of Alaska. Laboratory and field-estimated growth rates.

year	location	size range (mm)	temperature range	growth rate (mm/day	Reference
1981	Shekikof Strait	3 - 13	?	0.17	Kim & Gunderson (1989)
1983	"	6 - 15	5.5 - 7	0.21	Kendall et al. (1987)
1986	Auke Bay	4 - 13	6 - 7	0.23	Haldorson et al. (1989a)
1987	"	5 - 11	5.5 - 7	0.16	" " "
1988	"	5 - 11	6 - 7	0.22	" " "
1989	"	5 - 12	4 - 6.5	0.18	" " "
	laboratory	4 - 11	9.3 $\pm$ 0.5	0.20	Bailey & Stehr (1986)
	"	4 - 10	8 - 9	0.18	Bailey & Stehr (1988)
1989	Resurrection Bay	3 - 15	3.5 - 6.3	0.18	this study

can result in an earlier onset of phytoplankton and zooplankton blooms inside the fjord. Walleye pollock larvae thus might find better growth conditions inside the fjord early in the season.

In spite of the differences in temperature, stratification and vertical distribution, growth rates are similar in Shelikof Strait, Auke Bay and Resurrection Bay. The growth rates for Resurrection Bay were similar to those observed in the laboratory under optimal feeding conditions and at a higher temperature (Bailey and Stehr 1988, Table 11), suggesting that growth was not food or temperature limited in Resurrection Bay.

I detected no difference in growth rate between stations RES 2 and RES 4 in Resurrection Bay. This result is not surprising, given the proximity of the stations and the similarity in water properties. To test for interannual differences, data from additional years are needed. The potential for interannual variations in growth is high, since conditions in Resurrection Bay can be expected to be highly variable, due to the influence of large-scale and long-term events on the shelf as well as local and short-term events within the fjord. The nature and the timing of these events may vary greatly between years. If larvae enter the fjord from outside, the timing of events that carries larvae into the fjord will be especially important and may be critical for their success.

Differences in growth rates are most commonly attributed to variations in water temperature and prey concentration. The primary prey of first feeding walleye pollock are copepod nauplii ranging in length from 100 to 300 µm (Kamba 1977, Clarke 1978). Smith et al. (1991) found over 20,000 copepod nauplii (150-350 µm length) per m^3 throughout May 1988 in Resurrection Bay with numbers exceeding 100,000 per m^3 in mid-May. These prey concentrations are sufficient

for successful feeding of larval walleye pollock (Paul 1983, Haldorson et al. 1989b). If comparable prey densities existed in 1989 they would have provided sufficient prey for feeding success of pollock larvae, and the growth measurements suggest this was the case.

Competition for food is unlikely at the observed densities of pollock larvae and copepod nauplii. Laurence (1978) estimated a search volume of 10 liters per day for a 5 mm Atlantic cod (*Gadus morhua*), that is morphologically similar to walleye pollock. Even at the highest observed densities (12 larvae m^{-3}) only 120 liter per 1 m^3 of water per day would be searched by cod larvae. Ten liters of water contain upward of 200 nauplii at prey densities observed in May 1988 (Smith et al. 1991). The daily caloric requirement of first-feeding pollock larvae has been calculated as 76 nauplii (Yamashita and Bailey, 1989), a value that is much higher than estimates from field studies (Dagg et al. 1984; Clarke, 1978). Even the calculated requirement of 76 nauplii/day can easily be met by prey densities observed in Resurrection Bay in 1988. Thus the observed growth rates and prey concentrations suggest that growth of larvae in Resurrection Bay was not food limited.

Another important factor in regulating larval growth is temperature. Many studies have documented the effects of water temperature on growth of fish larvae (Houde 1989). Laboratory studies have shown that walleye pollock larvae reared at 5.5°C are more successful at capturing prey than larvae reared at 3°C (Paul 1983). Conversely at warmer temperatures larvae would have higher metabolic rates.

In our study temperatures in the larval environment ranged from 3.5 to 6.3°C. Thus there is a potential for temperature mediated differences in larval growth in Resurrection Bay. However, the

effects of temperature will be extremely difficult to measure due to vertical temperature gradients and horizontal advection of larvae. Minor changes in vertical position enable pollock larvae to regulate their thermal environment. Their ability to do so has clearly been demonstrated in laboratory studies, where larvae moved upward and away from cold (3°C) water introduced at the bottom of an experimental cylinder 150 cm deep (Olla and Davis 1990) and in nature they exhibit diel vertical migrations (Pritchett and Haldorson). A strong temperature gradient was present at all stations in Resurrection Bay at the time of sampling (Fig. 5), making it extremely difficult to estimate the average temperature experienced by larvae at any station.

Horizontal advection will also influence the thermal environment of larvae. Advection along isopycnals within the upper layer can carry larvae over water masses of different temperatures, especially if advected across the sill. Inside Resurrection Bay the upper layer is overlaying a water mass that is considerably colder than subsurface water on the shelf. Larvae in Resurrection Bay might have experienced a relatively wide range of temperatures during their short lifetime. Advection will affect growth in many other ways by exposing larvae to spatial and temporal variations in prey availability, predator abundance, and environmental conditions.

In summary, the evidence suggests that the Resurrection Bay area provides a suitable environment for the successful growth of larval walleye pollock. However, there is a high potential for interannual variability in this dynamic environment, and at present it is not clear whether Resurrection Bay is a reliable nursery ground every year. Changes in the timing of spawning and/or in the timing of events that establish favorable conditions for larvae in

the fjord can contribute to variations in growth and survival.

Hatching and spawning

Table 12 compares median hatch dates from Resurrection Bay and other areas around the Gulf of Alaska. The median hatch date is remarkably consistent among different parts of the Gulf and among different years. This seems to require an underlying, reliable mechanism that triggers spawning over such a broad geographical range. The values from Shelikof Strait suggest a trend towards later spawning dates between 1983 and 1987. More data are needed to see if a similar trend exists in other areas of the Gulf and to identify parameters responsible for the timing of spawning.

True hatch dates may be slightly earlier than estimated, because I could not correct for differential mortality with age. Median spawning could be later than estimated if hatching was still in progress at the time of sampling. This was indicated by the fact that larval size distributions were skewed towards smaller (younger) larvae (Fig. 19). Symmetry of the larval size distribution was tested using procedures described in Zar (1984). The distribution of all larvae in isopropyl alcohol and ethyl alcohol was significantly skewed (g_1=0.906, $p<0.001$, N=7835 and g_1=0.645, $p<0.001$, N=6284). However the same asymmetry will result from differential mortality since larger larvae experienced a larger cumulative mortality.

A discrepancy was found between the size of the smallest larvae captured and the size at hatching suggested from regression analysis. This discrepancy can have several possible causes. The smallest few percent of larvae may be much smaller than the average size at hatching. This would imply a very wide range of sizes at hatching. However, hatching size typically varies by no more than

Table 12: Median hatch dates of larval walleye pollock in the Gulf of Alaska

Year	Location	Hatch date	Reference
1983	Shelikof Strait	23 April	Yoklavich & Bailey (1990)
1985	"	23 April	"
1986	"	29 April	"
1987	"	2 May	"
1987	Auke Bay	28 April	Halderson et al.(1989a)
1989	Resurrection Bay	24/27 April	this study

about 1 mm (Nishimura and Yamada 1984, Bailey and Stehr 1986). The smallest 1% of larvae ranged from 3.03 to 4.04 mm in isopropyl alcohol and from 3.64 to 4.50 mm in ethyl alcohol. The average size of these larvae was 3.77 mm and 4.27 mm and may be a more realistic estimate of size at hatching. The y-intercepts of the regression equations thus seem to be too high and estimated growth rates may be smaller than the true growth rates.

If this is the case a more realistic growth rate may be obtained using a fixed y-intercept (size at hatching). This was modeled using linear regression analysis with a fixed size at hatching of 3.77 mm for larvae in isopropyl alcohol and 4.27 mm for larvae in ethyl alcohol. The resulting growth rates were 0.215 $\pm$ 0.010 mm/day (r^2=0.97) and 0.256 $\pm$ 0.016 mm/day (r^2=0.96). The high elevations of the original growth equations may be due to other factors like a systematic underestimation of age or fast growth during the first few days after hatching. Thus the former, more conservative growth estimates were used to estimate hatch dates.

Change in abundance

The change in abundance was probably overestimated due to net avoidance of larvae during the June cruise. During both cruises a mesh size of 505µ was used. While net avoidance cannot be quantified it is likely to be greater for the larger larvae present in June, resulting in underestimation of abundances. Further uncertainties result from the sampling design. Discrete depth sampling did not allow me to estimate abundances with high confidence. Thus the estimated change in abundance should be regarded as an approximation.

The estimated daily rate of change is similar to estimated

mortality rates for walleye pollock larvae in the field. Kim and Gunderson (1989) report a mortality rate of 0.09/d for early larvae in Shelikof Strait. However, the observed changes in Resurrection Bay do not reflect mortality due to predation and starvation alone but include changes in abundance due to advection. Advection can in fact play the major role in an open system like Resurrection Bay. The fact that the observed change in abundance is close to typical mortality rates indicates that advection did not remove all larvae from Resurrection Bay, whether they are spawned inside or advected into the fjord.

The question remains whether larvae stay inside the fjord during the late larval and juvenile stages. In Shelikof Strait, larvae remain planktonic until at least the end of July (Hinckley et al. 1991). As long as they stay planktonic, their distributions will be strongly affected by advection. Once they start to form schools and assume a more demersal lifestyle, they can maintain a distribution that is independent of advective processes. Juveniles that were spawned in Shelikof Strait are believed to enter inshore bays along the Alaska Peninsula after the planktonic stage (Hinckley et al. 1991). Resurrection Bay can play a similar role for juvenile walleye pollock. There are indications that at least some juveniles stay in the bay after the larval stage. In a survey of the benthos of Resurrection Bay in November 1977 and April 1978 Feder et al. (1979) found between 1 and 61 juvenile pollock 100 to 350 mm long in 10 min trawls with a small otter trawl.

CONCLUSIONS

The high abundances of larvae in Resurrection Bay indicate that the fjord is an important nursery ground for walleye pollock. Observed growth rates and prey abundances suggest that the fjord provides an environment that is well suited for successful growth and survival. The hydrography of the region and larval size distributions support the hypothesis that larvae recruit to the fjord from outside by advection into the outer basin of Resurrection Bay and across the sill. These observations and the high abundances observed in PWS during the same year (Norcross, unpubl. data) suggest that a large spawning population exists in the region and that not all walleye pollock in the northern Gulf of Alaska go to Shelikof Strait to spawn. Larval walleye pollock are also abundant in the bays of southeast Alaska (Haldorson et al. 1989a, b), thus it is likely that most of the embayments along the Gulf of Alaska act as nursery areas for this species.

Future work is needed to test whether Resurrection Bay is utilized as nursery ground every year or whether the abundances observed in 1989 were unusually high. While it is clear that the fjord was utilized by early larval walleye pollock in all three years for which samples are available, it remains unknown whether the fjord serves as a nursery ground for late larval and juvenile pollock as well. The biology of juvenile pollock is generally not very well understood due to the difficulties in sampling this age group. Nevertheless, Resurrection Bay, PWS and other bays along the coast of southcentral Alaska appear to play an important part in the life cycle of Gulf of Alaska pollock.

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